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Consequences of within- and between-group conflict in dwarf mongooses

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A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Doctor of Philosophy in the Faculty of Life Sciences

January 2021

School of Biological Sciences

Word count: 48,443

Summary

Conflict is rife in the natural world and is widely recognised as a powerful selective pressure in social evolution. For group-living species, conflict over valuable resources arises between members of the same group (within-group conflict) and with conspecific outsiders (between-group conflict; also called outgroup or intergroup conflict). Traditionally, research on nonhuman animals has focused on the contests that arise within- and between groups; in the former case, there have also been extensive studies of the immediate consequences of aggressive interactions. By contrast, relatively little is known about the short-term consequences of between-group conflict and, for both conflict types, there has been little empirical consideration of the longer-term consequences. In this thesis, I combine detailed behavioural observations, field experiments and long-term life-history data to investigate the consequences of within- and between-group conflict over different timeframes, using wild dwarf mongooses (*Helogale parvula*) as a model system. First, I show that unresolved within-group conflict can have cumulative behavioural effects and present evidence for delayed post-contest management by bystanders (Chapter Two). In the remaining data chapters, I focus on between-group conflict. I find consequences of outgroup threats in the short-term (in the hour after exposure) for within-group affiliation, foraging and sentinel behaviour (Chapter Three). I then demonstrate that such threats can also influence behaviour over longer timeframes, with carryover effects on affiliation into the following day, and cumulative effects on affiliation, foraging, sentinel and territorial behaviour, as well as body mass, after repeated outgroup encounters across a week. Lastly, I examine the reproductive consequences of between-group conflict and, unexpectedly, find a positive relationship with pup survival. By demonstrating an array of effects over timeframes rarely addressed previously, I help shed light on the more-lasting consequences of social conflict which is important for a greater understanding of how it shapes the lives of group-living species.

In loving memory of Peter

For a life full of adventure

Acknowledgements

From the UK to South Africa, I have been lucky to work with so many incredibly generous and inspirational people. Thank you to everyone for making the last four years an overwhelmingly positive experience.

There is one person in particular, to whom I would like to extend the most gratitude for his unceasing support throughout this whole process, Andy Radford. On countless occasions over the past four years his kindness has awed me and his intellect flawed me. I always come away from meetings with Andy feeling a lot clearer about the direction I'm headed, and with a renewed sense of optimism. He is always on hand to offer his expertise and moral support, whether I'm just down the corridor in the department or 10,000 miles away in the field. One of Andy's many talents is assembling teams of people who share a sense of humour, but also a genuine academic curiosity, ambition and respect for science. In many ways I have him to thank for introducing me to a number of the following people whom I also wish to thank.

Julie Kern established the Dwarf Mongoose Research Project (DMRP). For that feat alone I will have eternal respect for her. She has been a great friend and collaborator, and although she stopped working directly with the project in 2017, she has always been there for me when I have had questions, and there have been many! This probably goes some way to explaining why our voice notes are rarely shorter than 10 minutes, sorry about that. Something I have always appreciated from Julie is feeling able to vent during challenging times, and because she understands the work better than anyone, I never have to explain myself. I'm so happy that we managed to coincide our field seasons at the beginning of the PhD. Having Julie and Garth down the road on future trips was also such a treat – thank you for the many catch-ups over G&Ts and large glasses of vino!

The same can be said about Charlotte Christensen. Charlotte and I spent our very first field season on the project together back in 2013; an experience that cemented a life-long friendship and a new-found love for fieldwork in Africa. Charlotte is one of those friends who completely understands what I do and why, with a healthy mongoose obsession herself! I feel very lucky to have had her support throughout the PhD process. Charlotte was also the original dwarfie "poo-ninja", so I also have her to thank for introducing me to that less glamourous side of fieldwork.

None of this research would have been possible without Hennie, Eddie and Darnie Yeates. I would like to thank them for allowing us to work on their beautiful reserve. I would also like to extend my thanks to the friendly staff I overlapped with whilst working on Sorabi - Christoffel, Suzelle, James, Justice, Lindiwe and Petunia. From honey badgers raiding our bins and mysterious elephant break ins, to leopard kills, zebra meat collection and numerous flat tyres, we all experienced this rollercoaster together.

I would like to extend a huge thank you to the following people whom I overlapped with during three field seasons on the DMRP: Katie Collier, Emma Eastcott, Harry Suter, Alanah Lewis, Tecla Mohr, Izzy Jarrold, Sophie Manson, Jenny Linden, Josh Arbon, Emily Richens, Aidan Byrne, Hannah Rickets, Frazer Bayliss, Emily Grout, Alex Fergusen, Izzy Shan, Natalie Tegtman, Izzy Carpenter and Megan Layton. Thank you for always smiling, despite the lack of sleep, sweaty work and seemingly constant smell of egg! Special thanks go to Jenny Linden, without whom I may still be running the experiment in Chapter Four, to Natalie Tegtman for keeping me sane when it felt like everything was spiralling against me during my final field season, and to Megan Layton for managing the project amazingly through a global pandemic. Megan has also helped with project admin during the final month of writing up, for which I am extremely grateful.

I would also like to thank my surrogate family in South Africa for reminding me of the virtues of a good work/life balance. I have many fond memories of braiis and game drives with the following people, and am fully converted to celebrating Christmas in July! Thank you Katie, Andrew, Garth, Robbie, Rusty, Ed, Anka, Andre, Jen, Phil, Ann and Neil.

At this point it would be remiss of me not to thank the mongooses! Their quirky characters were a constant source of entertainment. A special thank you to Bean, and the fine supporting cast of Sorabi's rich wildlife, particularly Big boy, Elvis, Delilah and Gemima - a few of the resident ungulates.

Back in the UK I feel privileged to have been part of an inspiring group of people from the Universities of Bristol and Exeter, carrying out research spanning dwarf mongooses, fish and wasps. In 2020 the value of having this cohesive group of like-minded individuals to call on for support has been particularly apparent. Regular research group meetings on Zoom, virtual writing retreats and quizzes have all helped to keep morale up during this challenging time. There are a few people in particular whom I would like to thank for the help they have offered me: Patrick Kennedy is one of the smartest people I have ever met, and when it comes to Excel he appears to have a shortcut for absolutely everything. This has saved me an enormous amount of time. Ines Goncalves has also been a constant source of both technical and emotional support to me. I have an incredible amount of respect and gratitude for them both, as do I for Harry Harding. I look back very fondly on our daily coffee catch ups.

One the biggest challenges this year has been keeping calm whilst writing up throughout Covid-19. To this end I would like to thank my yoga instructor, Cae, for her regular sessions on Zoom. They have helped me immensely.

Last, but by no means least, my immediate family. I would like to thank mum and dad for installing a sense of adventure in me at a young age and for always encouraging me to do what I enjoy most and my sister for always being her smiley, optimistic, energetic self. Much gratitude to them and to Ros for their unwavering support throughout the PhD, and for sending regular care packages during the write up.

Closer to home, I would like to thank Jack for being the most effective stress reliever. Rescuing that dog was one of the best decisions we ever made. I also want to thank Mart for encouraging me to do this PhD in the first place, despite knowing that it would entail long periods apart. He has always been there to help me transition back into civilisation after each and every field season and has been my absolute rock throughout this whole process. The beautiful artwork that peppers this thesis is also thanks to him.

Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Chapter 1: General Introduction

All the photos that appear in this Chapter are my own unless otherwise indicated.

Thank you to Hannah Rickets for this photo of me and Benny.

1.1 Group-living

A fundamental question in behavioural ecology has been to explain why many animal species live in groups (Krause and Ruxton 2002). A group is defined as "any set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics" (Wilson 1975). Group-living has received considerable research attention from a wide-range of perspectives, including the conditions that favour its evolution, the benefits and costs of living in a group, the optimal group size and the mechanisms through which group-living is sustained (Krause and Ruxton 2002). Group-living evolves when the net benefits of associating with conspecifics exceed the costs. These trade-offs will vary between species and habitats, creating a wide range of social systems, each optimal for the environment in which the species lives (Lukas and Clutton-Brock 2017).

In part, group-living is thought to be an evolutionary response to predation risk as an individual's risk of predation generally decreases with increasing group size (Hamilton 1971). Reduced predation pressure arises for several, non-mutually exclusive, reasons that are encapsulated under the umbrella term 'safety in numbers'. One reason is the 'many eyes' hypothesis, whereby the likelihood of detecting a predator increases with group size as there are simply more individuals being vigilant (Lima 1995; Roberts 1996; Bednekoff and Lima 1998). Individuals can use their own personal vigilance to respond to predators or, when there is effective information transfer between individuals, they can respond to the antipredator behaviour (e.g. alarm signals) of other group members (Davis 1975; Beauchamp and Ruxton 2007). In some social species, there has been a further transition from collective to coordinated vigilance with the evolution of sentinel systems, where an individual adopts a raised position to scan for danger whilst groupmates engage in other tasks (Bednekoff 2015). With increasing group size, not only is there an overall increase in vigilance but individual investment declines without reducing the ability of the group to detect an approaching predator (Elgar 1989; McNamara and Houston 1992; Beauchamp 2008).

Group-living can also provide benefits when a predator attacks, through dilution and confusion effects as well as collective defence. In larger groups, the likelihood of an individual being attacked is diluted compared to those in a smaller group (Hamilton 1971). It is also harder for a predator to single out and attack one individual in a large group of similar-looking prey (Neill and Cullen 1974). Strong theoretical and empirical evidence exist for both these effects (reviewed in Lehtonen and Jaatinen 2016). For instance, it was recently shown that confusion effects are sufficient to explain the evolution of swarming behaviour (Olson et al. 2013). Individuals living in groups can also

employ collective defence when a predator attacks. By actively combining forces, many social animals are more successful at deterring predators than individuals would be alone (Cooper 1991; Fanshawe and Fitzgibbon 1993). An example of this is mobbing behaviour, which is found in a wide variety of birds and mammals (Owings and Coss 1977; Curio 1978; Graw and Manser 2007).

The other major driver of group-living is improved foraging efficiency (Clark and Mangel 1986). Animals living in groups can cooperate to catch prey that would be too large, elusive or dangerous for a single individual (Creel and Creel 1995). Cooperative hunting can involve complex behaviours where individuals adopt different roles to increase the chances of success (Stander 1992). Individuals searching for food can also benefit from being in a group by using the behaviour of others as a potential source of information. Group members can use inadvertent cues of recent foraging success (i.e. positioning of individuals) to locate a good foraging patch (local enhancement; Drent and Swierstra 1977; Poysa 1992), or individuals already at a foraging patch can gain information on patch quality from others (Templeton and Giraldeau 1995; Smith 1999). Moreover, a select number of species actively signal to group members the location of a food resource (Ward and Zahavi 1973), as seen in the famous honeybee (*Apis mellifera*) waggle dance (von Frisch 1967).

Whilst group-living generates antipredator and foraging benefits, as well as enhanced mate-finding prospects (Westneat et al. 2000), reproductive success (Silk et al. 2003), the ability to conserve heat through huddling behaviours (Andrews and Belknap 1986), and the potential to learn socially from the behaviour of group members (Heyes 1994), it is also associated with a variety of costs. For instance, larger groups are more conspicuous to predators (Uetz and Hieber 1994; Ioannou and Krause 2008), although the effect saturates above a certain size (Lindström 1989; Cresswell 1994). There is also an increase in competition over food resources (Janson 1985; Symington 1988; Isbell 1991). As group size increases, foraging patches are depleted quicker and each individual receives a smaller share; moreover, individuals can have food items aggressively stolen from them (Dolman 1995). Consequently, larger groups tend to spend more time foraging than smaller groups and travel a greater distance per day (Janson and Goldsmith 1995; Blumstein et al. 2001; Korstjens et al. 2006). Another cost for animals aggregating in groups is enhanced transmission of parasites and disease (Brown and Brown 1986; Hoi et al. 1998). In general, as groups grow in size, the costs of group-living increase until they outweigh the benefits. Hence, groups have an optimal group size (Pulliam and Caraco 1984), with many animals actively limiting the size of groups by refusing entry (Jordan et al. 2010) or evicting group members (Stephens et al. 2005).

Animals form groups that range hugely in size, composition and permanency (Krause and Ruxton 2002). In many cases, associations are relatively temporary—for instance, feeding aggregations—and such groupings can include thousands, or even millions, of individuals (Sinclair 1977; Simpson et al. 1999; Krause et al. 2000). However, in some species, individuals form relatively stable, more permanent compositions, such as those in cooperatively breeding species (Russell et al. 2007; Hatchwell 2009; Wong and Balshine 2011). If individuals are to form stable groupings, then they must overcome the inevitable conflicts of interest that arise and, hence, a variety of strategies have evolved to minimise the costs associated with competition between members of the same group (within-group conflict). Stable groups also offer a tempting range of resources that result in conflict with outsiders and, hence, a variety of behaviours have evolved in relation to competition with other groups (between-group conflict).

1.2 Within-group Conflict

Conflicts of interest between individuals in relatively stable groups are inevitable due to within-group heterogeneity; individuals of, for example, different sex, dominance rank, age, size and reproductive condition have conflicting preferences for optimising their fitness (Conradt and Roper 2009). Consequently, disagreements arise over food, mates, direction of travel, synchronisation of group activities and contributions to collective tasks (van Schaik and van Noordwijk 1986; van Schaik 1989; Menzel 1993; Conradt and Roper 2000). For instance, in long-tailed macaques (*Macaca fascicularis*), there are sex-based differences in foraging requirements and group movement is reduced when females carry young (van Schaik and van Noordwijk 1986); whilst in red deer (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*), opposite-sex group members have lower activity synchronisation than same-sex group members (Conradt 1998; Ruckstuhl 1998). Conflicts of interest generate unavoidable costs, especially if they escalate to physical contests (Hardy and Briffa 2013).

Costs of within-group contests vary considerably. Participants suffer time and energy costs, with resultant trade-offs against other activities such as foraging, and could also suffer from increased anxiety and damage to their social relationship (Aureli 1992, 1997; Silk 1997). In severe fights, individuals could incur injury and mortality costs, although the loser might be more at risk of these (Enquist and Leimar 1990; Chase et al. 1994). The loser could also be the target of renewed aggression, whilst other group members might suffer from redirected aggression and increased anxiety from viewing the contest (Aureli et al. 2002; Kazem and Aureli 2005; Judge and Bachmann 2013). Further, on losing a contest, individuals might be forced to leave the group and thus forfeit the benefits of group-living (Janson 1992). In these extreme circumstances, winners and non-participants might

suffer costs associated with reduced group size (e.g. less helping behaviour and greater predation risk) (Clutton-Brock et al. 1999, 2001). Given this array of potential costs, natural selection has favoured the evolution of conflict management strategies (Aureli et al. 2002). These act at two stages: strategies that prevent the escalation of conflict to physical aggression in the first place and strategies that mitigate or repair the damage after such escalation (Cords and Killen 1998; Aureli et al. 2002)

1.2.1 Conflict Prevention

The relative rarity of aggressive contests in social groups, despite the numerous conflicts-of-interest that arise, is a testament to the effectiveness of conflict prevention strategies (Aureli and de Waal 2000). Some potential within-group conflict is minimised by morphological and relatively fixed behavioural adaptations. For example, niche partitioning has evolved in some species to reduce foraging competition between individuals of different sex, age or dominance status (Selander 1966; Partridge and Green 1985). In the cooperatively breeding green woodhoopoe (*Phoeniculus purpureus*), males and females have different bill morphologies to exploit different food resources and minimise intersexual competition (Radford and Du Plessis 2003, 2004*a*). Dominance hierarchies within groups also help to regulate aggressive escalation by standardising priority of access to resources (Preuschoft and van Schaik 2000). For instance, in many species, such as wolves (*Canis lupus*), dominant individuals are the first to feed on a kill (Dale et al. 2017). Where extreme asymmetries in power exist, it has been further suggested that reproductive inhibition amongst subordinate females could be, in part, a mechanism to keep reproductive conflict under control (Schaffner and Caine 2000); when reproductive suppression ceased in cotton-top tamarins (*Saguinus oedipus*), aggressive interactions increased (Savage et al. 1997).

Animals living in stable groups also use a variety of more plastic behaviours to prevent physical aggression from arising. Vocal, visual and gestural signals are used in many social species to communicate dominance and submission (de Waal 1986). In general, threat signals are used to assert competitive ability and accentuate size and weaponry, whilst submissive signals reduce apparent size, conceal weaponry and act to appease the recipient, improving tolerance at a resource (Preuschoft 1992, 1999). For example, stumptail macaques (*Macaca arctoides*) use a mock-bite to indicate dominance, whilst chimpanzees (*Pan trylogytes*) use a vocal–gestural signal of subordination that involves pant-grunting and bending down (Preuschoft and van Schaik 2000). Elaborate greeting ceremonies, such as those in hamadryas baboons (*Papio hamadryas*; Colmenares 1990, 1991) and spotted hyenas (*Crocuta crocuta*; East et al. 1993) have also been suggested to have a conflict-

mitigation function, acting to reduce agonistic tendencies when individuals compete over reproductive females or reunite after temporary separation (Colmenares et al. 2000).

To investigate the behavioural strategies that animals employ to reduce the occurrence of within-group aggression, researchers have focussed their attention on two conflict-provoking conditions: crowding (competition for space) and scheduled feeding (competition for food) (Judge 2000). Correlational studies investigating the effects of crowding in primates have shown that they respond differently depending on the duration of exposure. In the short-term, there is often a reduction in overall activity as a possible conflict-avoidance strategy (Judge and de Waal 1993; Aureli et al. 1995); in the long-term, affiliative and submissive interactions increase as a possible tension-reduction strategy (Nieuwenhuijsen and de Waal 1982; Judge and de Waal 1997). In terms of food competition, captive studies (which can take advantage of scheduled feeding times) found that individuals increased their pre-feeding affiliative behaviours, such as grooming, sociosexual contacts or play, as a possible way of pre-emptively managing conflict (Mayagoitia et al. 1993; Koyama and Dunbar 1996; Palagi et al. 2006). More recently, an experiment on wild vervet monkeys (*Chlorocebus pygerythrus*) found evidence for such pre-emptive conflict management as individuals that groomed prior to the introduction of a food resource were less likely to act aggressively towards each other (Borgeaud and Bshary 2015).

Social species clearly adopt a variety of strategies to reduce the likelihood of a contest occurring. But, even when contests do arise, there are mechanisms to prevent further escalation. Ritualised escalation of conflict from signalling exchanges to physical fighting is a common strategy, allowing a combatant to withdraw if the costs become too high (Cullen 1966). In some species, third-party individuals intervene in contests, either aggressively or peacefully, attempting to bring the aggressive outbreak to an end (Petit et al. 1997). Similarly, in groups where one male defends a harem of females, dominant males have been reported to employ a policing strategy to keep conflict at bay (Oswald and Erwin 1976). Even with these strategies in place, though, physical aggression can intensify and, left unresolved, could have long-lasting and damaging consequences for dyadic relationships and group stability (Cords 1992; Matsumura and Okamoto 2000).

1.2.2 Conflict Resolution

Historically, it was thought that protagonists (former opponents) would avoid one another after fighting (Lorenz 1967). However, a study in 1979 changed the way that conflict between group members was viewed: Frans de Waal and Angeline van Roosmalen observed two captive chimpanzees,

that had just been involved in an aggressive interaction, come together, kiss and embrace each other. This gave rise to a new field of conflict management, termed conflict resolution, that focusses on the strategies that animals employ in the aftermath of a contest to reduce the costs of aggression (de Waal 2000). The interaction between those initially observed chimpanzees was labelled reconciliation and defined as 'the friendly reunion between former opponents not long after an aggressive confrontation' (de Waal and van Roosmalen 1979). Extensive research effort in the following three decades has led to the documentation of reconciliation in over 30 primate species (de Waal 2000; Aureli et al. 2002) and some non-primate species, including domestic goats (*Capra hircus*; Schino 1998), spotted hyenas (Wahaj et al. 2001), bottlenose dolphins (*Tursiops truncates*; Weaver 2003), wolves (Cordoni and Palagi 2008) and domestic dogs (*Canis familiaris*; Cools et al. 2008). Functionally, reconciliation has been shown to reduce the likelihood of renewed aggression, repair the relationship between opponents, restore tolerance to baseline levels and alleviate contest-induced stress (Cords 1992; Aureli et al. 2002; Silk 2002; Wittig and Boesch 2005; Arnold et al. 2010). Given the benefits, it is most likely to occur between opponents that have strong social relationships since the costs of unresolved conflicts are greater for these individuals (Aureli et al. 2002; Cords and Thurnheer 2010; Fraser and Bugnyar 2011).

Whilst a major focus of research on the post-contest behaviour of protagonists has been reconciliation, it is risky for some individuals to approach and affiliate with a former aggressor due to the possibility of renewed aggression. Further aggression between opponents could function to maintain or increase an individual's rank by signalling their fighting capabilities (Dugatkin and Druen 2004), or it could amplify winner-and-loser effects as reassertion of dominance could help to secure the outcome of future interactions (Chase et al. 1994). The risk of renewed aggression is thought to be more prevalent in species with more despotic social systems and rigid dominance hierarchies than those with more tolerant social systems (Sterck et al. 1997; Thierry 2000). Accordingly, in comparison to female Tonkean macaques (*Macaca tonkeana*), which have a relatively tolerant matrilineal society, female rhesus macaques (*Macaca mulatta*) exhibit less frequent reconciliation (Thierry 2000). In species such as rhesus macaques, avoidance of the former aggressor may be a more common post-contest strategy. There is some anecdotal evidence for post-contest avoidance in primates (Aureli 1992; Watts 1995), with more robust findings from Hanuman langurs (*Semnopithecus entellus entellus*; Sommer et al. 2002), meerkats (*Suricata suricatta*; Kutsukake and Clutton-Brock 2008) and rooks (*Corvus frugilegus*; Benkada et al. 2020).

Within-group contests can have consequences not only for the aggressor and victim but for other group members too. As research on conflict resolution increased, attention therefore shifted to interactions involving former opponents and bystanders (uninvolved third-party individuals). Most of this literature focusses on bystander-initiated interactions, especially with victims. In 1979, Frans de Waal and Angeline van Roosmalen also observed third-party individuals sometimes approaching and affiliating with the victims of aggression, which seemingly had a calming effect (although they did not test this function). This behaviour has subsequently been recorded in a variety of species, for example: primates, such as barbary macaques (*Macaca sylvanus*; McFarland and Majolo 2012), chimpanzees (Wittig and Boesch 2003; Fraser et al. 2008), western lowland gorillas (*Gorilla gorilla gorilla*; Cordoni et al. 2006; Mallavarapu et al. 2006) and bonobos (*Pan paniscus*; Clay and de Waal 2013; Palagi and Norscia 2013); canids, such as wolves (Palagi and Cordoni 2009; Baan et al. 2014) and domestic dogs (Cools et al. 2008); and corvids, such as rooks (Seed et al. 2007) and ravens (*Corvus corax*; Fraser and Bugnyar 2010). Convincing evidence was also recently found in prairie voles (*Microtus ochrogaster*; Burkett et al. 2016). There is ongoing debate as to the function of bystander-to-victim affiliation, with three prevailing hypotheses (Fraser et al. 2009). It could serve a self-protective function, reducing the likelihood of the bystander being the recipient of redirected aggression from a former protagonist (Call et al. 2002; Koski and Sterck 2009; Schino and Marini 2014). It could also substitute for reconciliation, whereby a bystander (kin or friend of the aggressor) offers affiliation to the victim in order to repair the relationship between the former opponents when reconciliation is too risky (Judge 1991; Wittig et al. 2007; Wittig and Boesch 2010). Lastly, bystander affiliation towards victims may function as consolation if the behaviour alleviates the post-contest anxiety of the victim (Fraser et al. 2008; Romero et al. 2010; Palagi and Norscia 2013; Burkett et al. 2016). The term consolation is now only used when there is convincing evidence for this hypothesis, which mostly stems from chimpanzees, bonobos and prairie voles (Fraser et al. 2008; Palagi and Norscia 2013; Burkett et al. 2016). Otherwise, the interaction is referred to as third-party, bystander or triadic affiliation. In general, there are differing amounts of evidence for each hypothesis, with the most pertinent likely dependent on the social system of the species in question. However, it is clear, that third-party individuals play an important role in post-contest management.

Bystanders can also initiate affiliative interactions with aggressors, although this aspect of post-contest behaviour has received comparatively little research attention. Approaching the aggressor is riskier than approaching the victim due to the greater possibility of receiving aggression (Koski and Sterck 2007). Functionally, there are some overlaps with bystander–victim affiliation. For instance, it could act to reduce anxiety (Das et al. 1998; Das 2000; Koski and Sterck 2007; Pallante et

al. 2018) or a bystander could reconcile with the aggressor on behalf of the victim (Romero et al. 2011; Yamamoto et al. 2020). Whilst there is some recent evidence for an anxiety-alleviation effect (Pallante et al. 2018), other studies have failed to find evidence for either of these hypotheses (Das et al. 1998; Koski and Sterck 2007; Romero et al. 2011). Bystander–aggressor affiliation could also function to strengthen alliances with aggressors, for which there is some evidence in chimpanzees (Romero et al. 2011). Moreover, it could appease the aggressor (van Hooff 1967), reducing arousal and the risk of further aggression (Judge 1991; Das 2000). Evidence for the appeasement hypothesis has been found in western lowland gorillas (Palagi et al. 2008), chimpanzees (Romero et al. 2011), Tonkean macaques (Pallante et al. 2018) and wolves (Cordoni and Palagi 2015). Appeasement and other post-contest management strategies related to victims (consolation, substitute reconciliation) occur more regularly in the absence of reconciliation between former opponents (Fraser et al. 2008; Palagi and Cordoni 2009; Pallante et al. 2018). Thus, in general, the benefits gained by third-party individuals interacting with former combatants outweigh the costs of leaving the contest unresolved. Although, it is important to note that some studies have failed to find any evidence for bystander–victim and bystander–aggressor affiliation (Aureli 1992; Verbeek and de Waal 1997; Romero et al. 2008), and it is likely that for some species different post-contest strategies such as avoidance are required.

In addition to the research showing how bystanders affiliate with victims and aggressors after a contest, a small number of studies have investigated the more general effects that within-group aggression can have on the group. For instance, in hamadryas baboons, self-directed behaviours (a reliable indicator of anxiety) increased among bystanders after a contest but decreased on witnessing reconciliation (Judge and Bachmann 2013). Bystander–bystander affiliation (also referred to as quadratic affiliation) has been demonstrated in the same species, along with Tonkean macaques, perhaps as a mechanism to reduce 'groupwide social tension' induced by aggression (Judge and Mullen 2005; De Marco et al. 2010). Evidence that this behaviour could also function as quadratic reconciliation, where the bystander kin of the aggressor affiliate with the bystander kin of the victim, was recently found in mandrills (*Mandrillus sphinx*; Schino and Sciarretta 2015). The same study also reported an increase in bystander–bystander aggression, likely due to social facilitation. Taken together, these studies highlight how aggressive interactions can have knock-on consequences for other group members.

1.2.3 Moving Forward

Much of the research that has been conducted on post-contest interactions, whether between former opponents, between bystanders and opponents or amongst bystanders, is observational, with a large

number of studies conducted in captivity (for exceptions of studies conducted in the wild, see Aureli 1992; Wittig and Boesch 2003, 2010; Wittig et al. 2007; McFarland and Majolo 2012; Baan et al. 2014). Moreover, the majority of studies consider the immediate consequences of aggression, focusing mainly on behavioural interactions in the 10-minute period after an aggressive episode. However, there is increasing evidence that earlier events can have lasting effects and that nonhuman animals use memories of previous interactions to inform later decisions (Seyfarth and Cheney 1984; Wittig et al. 2014; Kern and Radford 2018). Indeed, there is some experimental evidence that animals can use information from earlier affiliative interactions when deciding about whether to get involved in an aggressive interaction (Cheney et al. 2010; Borgeaud and Bshary 2015). They can also use information from earlier agonistic interactions to inform how best to respond to future aggression (Wittig et al. 2014; Tibbetts et al. 2020). These studies highlight that previous interactions (affiliative or aggressive) can be used to make decisions about involvement in conflict with a temporal delay. But, to my knowledge, there have been no studies considering whether resolution-related behaviours can also occur with a delay.

1.3 Between-group Conflict

From ants to primates, groups and their members come into conflict with conspecific rivals (referred to as between-group conflict, intergroup conflict or outgroup conflict) for a variety of reasons. For instance, outgroup males may attempt takeovers to monpolise breeding attempts, as seen in lions, (*Panthera leo*; Packer and Pusey 1983) and meerkats (Mares et al. 2012). Individuals may try to immigrate into a new group, either alone or in a same-sex coalition (Ridley 2012), to gain a higher-ranking position and be closer to the front of the breeding queue, as in dwarf mongooses (*Helogale parvula*; Rood 1990). Whole groups may invade territories to acquire access to resources, such as food, space and sleeping sites, or may attempt to annexe territorial space, as seen in chimpanzees (Wilson and Wrangham 2003; Mosser and Packer 2009; Mitani et al. 2010). The vast majority of research on outgroup conflict has focussed on what happens during interactions between rival groups (Radford 2003; Majolo et al. 2005; Kitchen and Beehner 2007; Crofoot et al. 2008). However, more recently, there has been increasing interest in the behavioural and fitness consequences of between-group conflict (Radford et al. 2016; Thompson et al. 2017; Lemoine et al. 2020*a*).

1.3.1 Interactions Between Rivals

In some species, such as bonobos, between-group interactions are largely peaceful (Lucchesi et al. 2020). In other species, such as mountain gorillas (*Gorilla beringei beringei*), at least some interactions between groups can involve affiliative behaviour among potential rivals (Mirville et al. 2018*a*). For

most species, many between-group interactions are neutral and entail simple information exchange about, for instance, group size and composition and thus potential dispersal and breeding opportunities (Radford 2003; Golabek et al. 2012). However, contests do arise between rival groups; as with within-group conflict, management strategies exist to minimise escalation to physical violence. Some between-group conflict is likely minimised by more-permanent strategies, such as group dominance hierarchies (Lemoine et al. 2020*b*), which could lead to smaller, less competitive groups avoiding the costs of contests they are unlikely to win (Smith and Parker 1976). When contests do occur, there is initial signalling—often visually and/or vocally (Radford 2003)—when rivals can determine the strength and motivation of their opponents. For example, green woodhoopoe contests take the form of vocal displays which can last for up to 45 minutes and involve over 100 vocal rallies (Radford 2003; Radford and Du Plessis 2004*b*). In most species, physical aggression is a last resort if a resolution cannot be found through less costly means. However, when such contests do arise, they carry large potential costs, including the risk of injury and death (Wrangham et al. 2006; Batchelor and Briffa 2011; Thompson et al. 2017).

The defensive actions of a group are influenced by the identity of the rival. For example, individuals, same-sex coalitions and whole groups pose different threats to particular group members. When individuals or coalitions attempt to gain dominance and breeding positions, the interests of group members are not perfectly aligned; some individuals have more to lose than others (Schindler and Radford 2018). Consequently, there can be considerable variation in defence, with aggressive responses usually sex-specific (Desjardins et al. 2008; Mares et al. 2011). By contrast, contributions to defence are usually more equal when rival groups are encountered as the threat is to shared resources, such as food or sleeping sites; there is a cost to all group members of losing the resource (Kitchen and Beehner 2007). Some variation in defensive contributions can still arise, though, as there remain differences in motivation and costs, as well as collective-action problems (Gavrilets 2015; Willems et al. 2015). Responses can also vary depending on whether the rival group is a neighbour or a stranger, a group from further afield (Christensen and Radford 2018). In some species, such as green woodhoopoes, strangers might represent more of a threat than neighbours ('dear enemy effect') as they could be seeking to take over the whole territory whilst neighbours may only invade temporarily (Radford 2005). In such cases, there is a reduced defensive response to neighbours cf. strangers, although there can still be variation depending on, for example, familiarity (Mirville et al. 2018*a*; Morrison et al. 2020). In other species, such as banded mongooses (*Mungos mungo*), neighbours can represent a greater threat ('nasty neighbour effect') as they provide intense competition and usually outnumber stranger groups (Müller and Manser 2007); defence against neighbours is therefore

stronger. The relative response to rivals can vary within populations depending on factors such as group density, the period of the breeding cycle, the frequency of intrusions and encounter location (Christensen and Radford 2018).

Along with variation in defensive actions due to differences in intruder identity, there is extensive evidence for variation in participation based on individual characteristics, especially sex and dominance status (Heinsohn and Packer 1995; Kitchen and Beehner 2007). Since the interests and motivations of group members differ, so do the costs and benefits of engaging in an outgroup contest (Milinski and Parker 1991; Packer and Pusey 1997). Males are predicted to be more likely to contribute to defence when their breeding position or access to females is threatened ('male mate-defence hypothesis'; Trivers 1972; Fashing 2001); support for this relationship has been found in many primate species (reviewed in Kitchen and Beehner 2007). As female fitness is largely limited by nutrition (Trivers 1972), their contribution to defence is predicted to be more likely when foraging resources are at risk ('female resource-defence hypothesis'; Fashing 2001). An early study on Tana River mangabeys (*Cercocebus galeritus*; Kinnaird 1992) found evidence for this association, but demonstrating a link between resources and contest participation has proven difficult in many species (Kitchen and Beehner 2007). Dominance status also influences participation in outgroup contests; depending on the social system, higher-ranking or lower-ranking individuals could have more to lose, which is mirrored in their levels of contribution (Nunn 2000). In some species, where high rank confers better access to food and mates, these individuals participate more (Cooper et al. 2004; Arseneau-Robar et al. 2016; Langergraber et al. 2017). By contrast, in cooperatively breeding species where intruders threaten the linear position of a subordinate in a breeding queue, those lower-ranking individuals may contribute more to defence (Cant et al. 2002; Radford 2003). Whilst defence of mates and food explains much between-sex variation in participation, it is rank and reproductive access that are often important in explaining within-sex variation (Kitchen and Beehner 2007).

Considerable research has also examined the factors that influence the outcome of contests (i.e. who wins and who loses). The competitive ability of a group (also referred to as the resource-holding potential) is often correlated with group size (Crofoot et al. 2008) and many species seem able to assess the number of opponents in a potential contest (McComb et al. 1994; Hauser 2000). Indeed, there is evidence from a variety of taxa showing that relative group size is an important factor in determining the outcome of contests, with larger groups more likely to win than smaller groups in, for example, primates (Wilson et al. 2001, 2012; Kitchen 2004; Roth and Cords 2016), mongooses (Cant et al. 2002; Dyble et al. 2019) and birds (Radford and Du Plessis 2004*b*). In some cases, the composition

of participants is a better predictor of outcome than group size. For example, in wolves, groups are more likely to win if they have a greater number of older individuals or adult males participating, even if they are the smaller group (Cassidy et al. 2015); the relative number of adult males seems to influence the outcome in many species (Kitchen et al. 2004; Mosser and Packer 2009; Harris 2010; Markham et al. 2012). Another key factor is contest location, with many studies documenting an interactive effect between location and group size (Crofoot et al. 2008; Furrer et al. 2011; Markham et al. 2012; Strong et al. 2018). For instance, smaller groups can defeat larger groups when the contest occurs towards the centre of their territory. This is likely due to differences in perceived threat, with more to lose when contests occur in the core of a territory, leading to an increased investment in defence (Crofoot et al. 2008).

1.3.2 Consequences of Between-group Conflict

Compared to our understanding of contests themselves, much less is known about the wider consequences of outgroup conflict (Radford et al. 2016). As with predation (Creel and Christianson 2008), whilst the most obvious consequences arise from contests with rivals, especially if they escalate to violence (Boesch et al. 2008), outgroup conflict could have a broader influence. For example, there can be effects from encountering secondary cues (e.g. faecal deposits) of rival presence (Christensen et al. 2016) or as a result of being in areas of likely conflict (Radford 2011). The overall risk of outgroup conflict (e.g. the number of territorial neighbours or the likelihood of intrusions) and cumulative build-up of events could also have behavioural and fitness consequences (Thompson et al. 2017; Lemoine et al. 2020*a*).

Theory predicts that outgroup conflict should affect subsequent within-group behaviour (Hamilton 1975; Alexander and Bargia 1978; Reeve and Hölldobler 2007). Over the past five years, there has been increasing interest in the effect that outgroup conflict can have on within-group aggression and affiliation, both during and after actual contests or interactions with cues to the presence of a rival group. Investigations of vervet monkey behaviour during outgroup contests found that males use aggression to coerce and punish those individuals attempting to instigate and escalate the conflict into costly fights (Arseneau-Robar et al. 2018). An increase in within-group aggression during outgroup interactions has also been reported in the cichlid *Neolamprologus pulcher*, possibly as an incentive to increase current efforts in defence (Braga Goncalves and Radford 2019); a strategy which has also been reported in vervet monkeys (Arseneau-Robar et al. 2016). In principle, increased within-group aggression following outgroup contests could function to punish free-riders (Radford et al. 2016). However, there is little evidence of this – studies that have examined post-contest within-

group aggression have tended to find no significant increase (Nunn and Deaner 2004; Bruintjes et al. 2016). One study did report an increase in aggressive interactions immediately after contests in bonnet macaques (*Macaca radiata*), but since this increase was due to males targeting females, herding behaviour was suggested as the possible function: males attempting to discourage emigration and/or mating with individuals in different groups (Cooper et al. 2004). In fact, some very recent studies have reported a reduction in within-group aggression in the aftermath of an outgroup threat (Mirville et al. 2020; Preston et al. 2020; Samuni et al. 2020). This has been interpreted as a possible conflict management stratetegy, to promote group cohesion during periods of external conflict.

Short-term alterations in affiliative behaviours have been documented during and following exposure to outgroup threats. For example, affiliation is used by female vervet monkeys to promote male participation in current contests (Arseneau-Robar et al. 2016). Some studies have found evidence for a reduction in grooming after experiencing outgroup threats, likely due to trade-offs with other activities such as scent-marking and foraging (Preston et al. 2020; Yi et al. 2020). However, there is a growing body of evidence showing that within-group affiliation increases after encountering intruders. Early correlational data on female blue monkeys (*Cercopithecus mitis*) and samango monkeys (*Cercopithecus mitis erythrarchus*) found that grooming increased in the 10 minutes after territorial interactions (Cords 2002; Payne et al. 2003). These findings were supported by observational studies on green woodhoopoes and mountain gorillas looking in the hour after an outgroup contest (Radford 2008*a*; Mirville et al. 2020). Captive experiments on fish and invertebrates have also demonstrated the same effect (Bruintjes et al. 2016; Birch et al. 2019). However, only one experimental study has provided evidence for this relationship in natural conditions: Radford (2008*b*) found that green woodhoopoes increased their allopreening more following playback of vocal choruses from non-neighbouring groups compared with those from neighbouring groups. Proximally, affiliation is predicted to increase following outgroup interactions to reduce conflict-induced anxiety, since both the giving and receiving of grooming is known to have this benefit in mammals and birds (von Holst 1998; Aureli et al. 1999; Aureli and Yates 2010; Radford 2012). Functionally, post-contest affiliation may be used as a reward and to strengthen social bonds, possibly promoting participation in future contests (Radford et al. 2016).

Changes in behaviours other than affiliation and aggression are expected in response to outgroup conflict (Radford et al. 2016). One area that has received some attention is group movement. For instance, white-faced capuchin monkeys (*Cebus capucinus*) travelled further and faster after losing a contest compared to when they won (Crofoot 2013). Likewise, mountain gorillas increased the

distance they travelled on days when they encountered a rival group (Seiler et al. 2018). One study found no difference in group movement before and after outgroup contests in wild dogs (*Lycaon pictus*; Jordan et al. 2017), whilst dwarf mongooses were shown to reduce their distance and speed after the discovery of secondary cues (faecal deposits) indicating the presence of a rival group (Christensen et al. 2016). Such variation likely reflects differences arising from encountering actual intruders versus cues of their presence, and the different costs and benefits linked to the outcome of a contest. For instance, groups that lose may be temporarily excluded from an area or decide to avoid the zone of conflict altogether (Crofoot et al. 2013). Investigations of group activity patterns have also revealed alterations post-contest (Mirville et al. 2020; Yi et al. 2020). Javan gibbons (*Hylobates moloch*) spent more time foraging after encountering an opposing group, potentially to offset the increased activity costs associated with a contest (Yi et al. 2020), whereas mountain gorillas showed no difference in the amount of time dedicated to foraging pre-and-post-conflict, likely due to the abundance of food in the area (Mirville et al. 2020). Compared to group actions, assessing differences in individual behaviours is harder due to the detailed data collection required, often in challenging field conditions. Whilst research on individual and pair-bonded territory holders has shown, for instance, increased vigilance folllowing territorial intrusions (Olendorf et al. 2004; Descovich et al. 2012), experimental tests of such effects have not been conducted in group-living species.

Most research investigating the behavioural consequences (within-group interactions, group movement and activity patterns) of outgroup conflict has focussed on short-term effects (usually within 1 hour) after single interactions with outsiders or cues of their presence. Evidence for longer-term effects on behaviour is limited, in part due to the logistical challenges of assessing changes over longer timeframes. Some observational studies have shown that resource-use decisions can be disrupted the evening following a daytime outgroup contest (Crofoot 2013; Radford and Fawcett 2014; Dyble et al. 2019). Specifically, the occurrence of between-group interactions during the day affected where groups chose to sleep in the evening. In green woodhoopoes, groups that engaged in an extended between-group contest in the morning were more likely to roost in that area in the evening, even if they had lost the contest (Radford and Fawcett 2014). In meerkats, losing groups were more likely to move sleeping burrow than winning groups, and on moving they travelled closer to the core of their territory, whilst winning groups moved closer to their rival's territory (Dyble et al. 2019). Other correlational studies have found evidence for longer-term changes in territory use. For instance, yellow baboon (*Papio cynocephalus*) groups that won contests did not change their space use, but groups that lost used the area surrounding the encounter location less in the following three months (Markham et al. 2012). Addressing the longer-term behavioural effects of outgroup conflict—both

those arising from single events and cumulative effects of multiple events and the overall threat (Samuni et al. 2020)—is important for bridging the current gap between evolutionary theory and empirical work on behavioural traits.

Ultimately, outgroup conflict can have fitness consequences. There are clear potential costs from physical contests between groups, including loss of life, changes in breeding positions and extra-group matings. One of the most extreme examples occurs in chimpanzees, where males undertake boundary patrols into neighbouring territories and have been observed attacking and killing individuals in rival groups (Goodall et al. 1979; Wilson et al. 2014). Raids with the apparent intention of killing dependent young have also been observed in banded mongooses (Cant et al. 2002) and greater anis (*Crotophaga major*; Strong et al. 2018). More commonly, mortality is the result of being attacked in violent outgroup contests, which have been reported in many taxa, for instance: primates (Gros-Louis et al. 2003; Aureli et al. 2006; Rosenbaum et al. 2016), carnivores (Mosser and Packer 2009; Cassidy et al. 2015; Jordan et al. 2017; Thompson et al. 2017; Dyble et al. 2019), birds (Hannon et al. 1985) and insects (Batchelor and Briffa 2011; Rudolph and Mcentee 2016). Immediate reproductive costs could arise from interactions with outsiders if a dominant individual is usurped and loses its breeding position (Packer and Pusey 1983; Fedigan 2003; Beehner and Bergman 2008). Additionally, extra-group matings have negative consequences for the dominant male that loses paternity. In some species, such as African striped mice (*Rhabdomys pumilio*) and meerkats, subordinate males temporarily leave their group and rove between groups seeking out mating opportunities over the breeding season (Schradin and Pillay 2005; Young et al. 2007). In other species, individuals sneak matings during contests, as in common marmosets (*Callithrix jacchus*) and banded mongooses (Lazaro-Perea 2001; Nichols et al. 2015; Johnstone et al. 2020).

Outgroup contests can also have delayed fitness consequences for both participants and non-participants. For instance, animals injured in contests could experience a greater mortality rate or reduced reproductive performance (Bernado and Agosta 2005; Krause et al. 2017). After a change in male breeding position, infanticide might be enacted by the new breeder to bring females into oestrus sooner, with clear negative consequences for the young and their parents (Packer and Pusey 1983; Fedigan 2003; van Belle et al. 2010). Incoming breeders of both sexes sometimes evict existing group members, be it former breeders and their allies or independent offspring (Mares et al. 2012). Evicted individuals subsequently suffer costs associated with being alone or in small groups (Packer et al. 1988; Ridley et al. 2008; Young and Monfort 2009), such as reduced foraging success, increased predation risk and fatal encounters with rival groups (Cant et al. 2001; Ridley et al. 2008; Kingma et al. 2016).

There is also clear evidence that time spent outside the safety of groups can have negative effects on longevity (Cram et al. 2018). Fitness consequences could also arise from spatial and behavioural changes resulting from outgroup contests. For example, if losing groups are temporarily excluded from part of their territory or decide to avoid the area altogether, they might be reliant on lower-quality parts of their range that have fewer food resources or a higher risk of predation (Mitani et al. 2010; Markham et al. 2012; Crofoot 2013). This could have knock-on consequences for survival, but also current and future reproductive success if there is a reduction in parental care (Mares et al. 2012) or if adult body condition declines (Wey et al. 2015). Furthermore, outgroup interactions, particularly those that are violent, could aid the transmission of disease and parasites (Drewe 2010; Craft et al. 2011), with clear survival costs for individuals who contract the disease or high parasite load (Milinski 1985; Robar et al. 2010). The majority of studies assessing the fitness consequences of outgroup conflict focus on this array of immediate and delayed costs to individuals of single contests. However, cumulative effects could arise from the recurrent nature of outgroup contests.

In the wild, outgroup interactions occur repeatedly over time and, as with other stressors, an increase in outgroup threat level could result in chronic stress (Samuni et al. 2019). Chronic stress is associated with a reduction in body condition and increased mortality (Pride 2005; Wey et al. 2015) due to, for example, increased vulnerability to disease and predation (Romero et al. 2009; Vuarin et al. 2019). Chronic stress may also disrupt reproduction. For instance, it can lead to a reduction in breeding rates (Mileva et al. 2011; Dulude-de Broin et al. 2020), the number of young (Boonstra et al. 1998), offspring size (Dantzer et al. 2018) and offspring survival (Eriksen et al. 2015). Two studies have specifically considered the cumulative pressure of outgroup conflict on reproductive success. High rival neighbour pressure in chimpanzees, decreased the probability of offspring survival during pregnancy and led to longer inter-birth intervals (Lemoine et al. 2020*a*), and between-group interactions in banded mongooses decreased pup survival; litters were less likely to emerge if there had been a contest shortly after birth (Thompson et al. 2017). Given the range of direct and delayed fitness consequences (paragraphs above), there is a need for further work considering the cumulative fitness consequences arising from outgroup conflict, particularly in species which have less severe outgroup interactions: contests in chimpanzees and banded mongooses are regarded as some of the most violent in the animal kingdom (Johnstone et al. 2020).

1.3.3 Moving Forward

After an extensive effort documenting how animals behave during outgroup interactions, research interest has recently grown in the behavioural and fitness consequences of outgroup conflict.

However, the scope of these studies has so far been limited. Work is needed on how outgroup conflict can affect a broader range of behaviours, particularly at the individual level. There is also a need for experimental studies conducted in natural conditions to examine the consequences of outgroup conflict across different timeframes, including carryover effects into the following day, and also whether cumulative effects can arise from repeated conflicts, since this is the more realistic scenario for animals in the wild. There is also the potential for outgroup conflict to impact individual fitness, not just through immediate and delayed effects on survival, but through the cumulative effects of stress on reproductive success. A better understanding of the longer-term behavioural and fitness consequences will help shed light on the role and importance of outgroup conflict in social evolution.

1.4 Dwarf Mongooses

1.4.1 Dwarf Mongoose Biology

The dwarf mongoose belongs to the order Carnivora and family Herpestidae, in which there are 34 species (Schneider and Kappeler 2014). These small, terrestrial carnivores have a distribution spanning Asia (eight species) and Africa (26 species), but the social organisation is only known for 19 of these species (Veron et al. 2004; Schneider and Kappeler 2014). Of these, 11 are solitary and eight are group-living, with three of the latter described as highly social due to their stable social groups and cooperative breeding: meerkats, banded mongooses and dwarf mongooses (Schneider and Kappeler 2014). Dwarf mongooses are the smallest of these three (250–300 g; Rood 1986), with a distribution from southern Ethiopia to north-eastern South Africa (Sharpe 2015).

Dwarf mongooses form large groups (5–30 individuals) comprising a dominant breeding pair, several subordinate adult helpers of both sexes, and pups (Schneider and Kappeler 2014). Strong linear dominance hierarchies exist within each sex, with rank positively correlated with age (Creel et al. 1992); there is no sexual size dimorphism (Sharpe et al. 2012). Females are largely philopatric, remaining in their natal group and queuing for the dominant position, although they occasionally disperse if there is a high-ranking position available in nearby groups (Rood 1990). Males usually disperse around 2–3 years of age, either singly or in a same-sex coalition (Rood 1987, 1990). For both sexes, immigrants attain dominance and thus direct fitness benefits earlier than those in their natal groups (Rood 1987, 1990).

The dominant pair monopolise reproductive opportunities and are the only individuals guaranteed to reproduce (Rood 1980; Keane et al. 1994). Reproduction is seasonal, occurring in the summer months to coincide with the period of greatest rainfall (Rood 1980, 1983). Over the breeding

season, two to three litters (occasionally four) are produced (Rood 1980). The dominant female always comes into oestrus (up to seven days long) and is mate-guarded by the dominant male over the majority of her cycle (Rood 1980). Other high-ranking subordinate females can come into oestrus in synchrony with the dominant female and occasionally become pregnant; in one population, 12% of subordinates became pregnant per year (Creel and Waser 1991; Creel et al. 1992). Lower-ranking subordinate females are endocrinologically suppressed whilst males are behaviourally suppressed by instances of male–male aggression (Creel et al. 1992). The gestation period in dwarf mongooses varies from 49 to 56 days (Rasa 1977; Rood 1980), after which a litter ranging from one to six individuals is born underground, usually in termite mounds (Rasa 1977; Rood 1978, 1980). It is thought that most of a subordinate female's offspring are lost due to infanticide by the dominant female (Rasa 1973*a*; Rood 1980), although in one population, subordinate females accounted for 15% of all young (Keane et al. 1994). Subordinate females that were pregnant and lost their young can allolactate (Keane et al. 1994), and instances of spontaneous lactation have also been reported from females that were not observed to be pregnant (Rood 1980; Creel et al. 1991). Subordinates of both sexes help raise the offspring by babysitting (guarding), feeding, grooming and carrying the young (Rasa 1977; Rood 1978).

Dwarf mongooses are diurnal and territorial, with territory sizes ranging from 0.65 to 0.96 km^2 (Rasa 1987). Groups occupy savannah and woodland habitat, typically characterised with numerous termitaries, which they use as refuges to sleep in at night and as sanctuaries to escape danger during the day (Hiscocks and Perrin 1991; Kingdon 2015; Figure 1.1). Individuals frequently engage in allogrooming behaviour whilst groups are stationary at these refuges (Kern and Radford 2018; Figure 1.2a). Group members typically emerge from their sleeping burrow shortly after sunrise and travel together within their home range, feeding mainly on invertebrates (e.g. crickets, grasshoppers, termites, spiders, centipedes and millipedes), but occasionally small mammals, birds and lizards (Rasa 1973*b*; Kingdon 2015). Foraging is carried out independently (there is no cooperative hunting or prey sharing), with individuals scratching through the soil and digging in a head-down position (Rasa 1973*b*; Figure 1.2b). This position, coupled with their small size, makes dwarf mongooses highly vulnerable to predation (Rood 1986). They have therefore evolved an elaborate vigilance system where, as well as individually pausing to scan their surroundings whilst foraging, a sentinel is often posted: this individual adopts a raised position to look out for danger (Rasa 1986, 1989; Kern and Radford 2013; Figure 1.2c).

Figure 1.1 A dwarf mongoose group having just emerged from their overnight refuge.

Dwarf mongooses are highly vocal and have a wide repertoire of over 30 different call types (Manser et al. 2014). When a predatory threat is spotted, alarm calls are used to alert the rest of the group. These calls differ depending on whether it is an aerial or terrestrial predator enabling the appropriate behavioural response (Beynon and Rasa 1989; Collier et al. 2017, 2020). Individuals produce regular close calls (also referred to as contact calls) whilst foraging and moving to maintain group cohesion (Sharpe et al. 2013), and when on sentinel duty emit a 'watchman's song', which informs foraging group members of their presence and allows individuals to lower their investment in personal vigilance (Rasa 1986; Kern et al. 2016). Recruitment calls are used to bring the group together and elicit a mobbing response when snakes or other ground-dwelling threats (e.g. rock monitors, *Varanus albigularis*) are encountered (Kern and Radford 2016; Rubow et al. 2017*a*). Lost calls (also referred to as isolation calls) are produced when a group member becomes separated from the group and during intergroup encounters (Rubow et al. 2017*b*, 2018). All these calls are used to coordinate their cooperative behaviours.

Figure 1.2 Two dwarf mongooses engaged in allogrooming behaviour (a), an individual foraging in a head-down position (b), and an individual on sentinel duty (c).

Within-group conflict in dwarf mongooses has two main forms: conflict that arises over dominance and reproduction, and conflict that arises over food. Compared to meerkats, reproductive and dominance-related conflict is less severe in dwarf mongooses. There is no eviction of pregnant subordinate females over the breeding season, for example, and when a dominant individual dies the position is taken up relatively peacefully by the next in line (Rasa 1987), as opposed to fighting for the position (Spong et al. 2008). Serious fights between individuals are rare, and instead aggressive interactions mainly involve a combination of chasing, cheek-marking and threat-scratching (Rasa 1973*c*, 1987). These interactions increase in frequency over the breeding season; for instance, male–male aggression more than triples during mating periods as a result of the dominant male trying to mate-guard the dominant female (Creel et al. 1992). Occasionally, when a group member becomes sick or injured, another individual might seize the opportunity to gain rank (usually females that queue for the dominant position in their natal group), and a series of fights occur often resulting in rank reversals (Sharpe et al. 2013). However, the most common agonistic interactions in dwarf mongooses are those arising over food. Foraging displacements occur throughout the year but are more common over the winter months when prey density declines (Sharpe et al. 2016). In these situations, a higher-ranking group member (not restricted to dominants) approaches a foraging group member that is lower in rank, usually an individual who is digging in a head-down position and commandeers the foraging hole or directly steals the prey item. This sequence is usually accompanied with the aggressor producing deep growls and hip-slamming the victim out of the hole; this displaced individual then retreats whilst submissively squealing (Sharpe et al. 2013, 2016).

Outgroup conflict in dwarf mongooses also takes two main forms: indirect defence when scent-marking at communal latrines and direct defence when rival groups are encountered. Although scent-marking can have a within-group function, it also plays a key role in outgroup defence, allowing

the gathering of information on rivals without having to engage in potentially dangerous contests (Sharpe 2015). Latrine sites include large boulders, rock overhangs, dead logs, parts of termite mounds and small bushes (Sharpe et al. 2012). Four olfactory channels are used to signal their presence at latrines: faeces, urine, cheek-gland and anal-gland secretions (Rasa 1973*c*). Cheek-gland secretions are deposited by rubbing the sides of their cheeks against a surface, whilst anal-gland secretions are deposited by either adopting an anal-drag or handstand position (Sharpe et al. 2012). The latter entails flinging their back legs behind themselves to catch hold of a substrate, standing on their forelegs and rubbing their anal gland along a horizontal or upright surface (Sharpe et al. 2015). These secretions are individually identifiable and have been shown to remain detectable for 20–25 days in captivity (Rasa 1973*c*; Decker et al. 1992). In the wild, it takes a group around 25 days to traverse their territory (Rasa 1987) and latrines are regularly re-visited, with all group members participating in the activity (Sharpe et al. 2012). It has also been shown that during a latrine event, males are more likely to handstand than females and smaller males exaggerate the height of their anogenital deposits, possibly to mislead rival males (Sharpe et al. 2012; Sharpe 2015).

Territorial incursions can occur by individual intruders, coalitions of dispersing males, prospecting males, neighbouring groups or transient (stranger) groups. When dispersing males attempt to emigrate into a new group, aggressive interactions ensue which involve lots of chasing and fighting by resident males (Rood 1990; Creel 1993). Consequently, male coalitions can only join groups containing low numbers of resident males (Rood 1990). When rival groups are encountered, contests vary in severity from signalling exchanges (mainly acoustic) with only a couple of individuals involved to violent confrontations with all group members chasing and fighting (Rasa 1987, personal observation). Most intergroup encounters have a vocal component, with individuals in both groups giving close and lost calls at high rates (personal observation). Group size normally determines the outcome: small groups usually try to avoid large groups, but interactions between similar-sized groups often escalate to violence (Sharpe 2015). Early work by Anne Rasa indicated that groups respond differently to intrusions by neighbouring groups and transient groups (Rasa 1987). Sleeping burrows located on border zones are regularly contested between neighbouring groups, whereas interactions with stranger groups (splinter groups or newly established groups seeking a territory) usually involve fighting and the latter being chased away (Rasa 1987). Encounters with both types of group are accompanied with a post-interaction latrine frenzy (Rasa 1987). Adult individuals are rarely injured during outgroup fights, but juveniles can become lost in the melee and if they end up with the rival group are usually attacked (Rasa 1987, personal observation).

1.4.2 Study Site

This research was conducted on Sorabi Rock Lodge, a 4 km^2 private game reserve located 388–514 m above sea level in the Limpopo Province of South Africa (24° 11'S, 30° 46'E). The habitat is classified as part of southern Africa's Savannah Biome and the lowveld climate has two distinct seasons (Figure 1.3). Normally, the summer months span from September to April and are defined by high temperatures (average daily maximum for February, the hottest month: 34.6°C) and the majority of the annual rainfall (average annual rainfall: 467 mm; September 1998–May 2012), while the winter months of May to August are colder (average daily maximum for July, the coolest month: 25.7°C) and a lot drier (Kern 2012; Kern and Radford 2013). There are no rivers on Sorabi, but it does contain several small ravines which often flow after large downpours in the summer. There are also five small dams, which are regularly pumped by borehole during the winter months. Most of the reserve is gently undulating, although three large granite outcrops border the reserve (Figure 1.3).

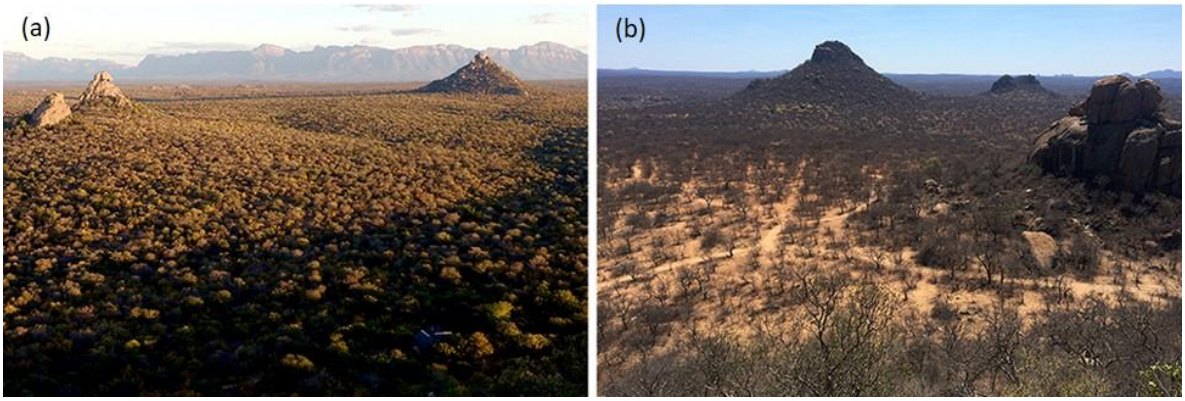

Figure 1.3 The site of the Dwarf Mongoose Research Project, Sorabi Rock Lodge, in the summer (a) and winter (b).

The vegetation on Sorabi is dominated by a number of bush-encroaching species, owing to its past as a cattle farm (Kern 2012). Common tree species on the site include velvet corkwood (*Commiphora mollis*), marula (*Sclerocarya birrea*), knob thorn (*Acacia nigrescens*) and red bush willow (*Combretum apiculatum*). Grassy areas are scarce, but mainly consist of species belonging to the *Aristida* and *Eragrostis* genera. Large expanses of low-lying shrubs are abundant, typically comprising species such as *Pechuel-loeschea leubnitziae, Abutilon angulatum* and *Heliotropium steudneri* (Kern 2012). The reserve is home to a wide array of fauna, with frequently encountered animals including giraffe (*Giraffa camelopardalis*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and zebra (*Equus burchellii*) (Kern 2012). However, many more elusive species present a particular threat to dwarf mongooses. For example, terrestrial predators in the area include black-backed jackals (*Canis mesomelas*), side-striped jackals (*Canis*

adustus), honey badgers (*Mellivora capensis*), African civets (*Civettictis civetta*), servals (*Felis serval*), African wildcats (*Felis lybica*), caracals (*Caracal caracal*) and slender mongooses (*Galerella sanguinea*), along with a number of reptilian species (Sharpe et al. 2010; Kern 2012). Dwarf mongooses are also at risk from predation by large diurnal raptors, of which the African fish-eagle (*Haliaeetus vocifer*), brown snake-eagle (*Circaetus cinereus*), tawny eagle (*Aquila rapax*) and black-chested snake-eagle (*Circaetus pectoralis*) are regularly seen (Kern 2012).

1.4.3 Study Population

The Dwarf Mongoose Research Project (DMRP) has been monitoring a population of wild dwarf mongooses since 2011. Over my PhD study period (January 2017 to January 2020), the population fluctuated between five and eight groups: one group went extinct, another likely dispersed under the fence line and three new groups were habituated. Each group has their own distinct territory on different sections of the reserve and range in size from 2 to 24 individuals. Study groups are habituated to human presence, allowing undisturbed observation on foot from <5 m (Kern and Radford 2013, 2014). All animals are individually recognisable either through small blonde dye marks on their fur (Garnier Nutrisse; Figure 1.4a), applied using an elongated paintbrush, or through natural distinguishing features, such as a scars, stumpy tails or missing limbs. Adults are classified as individuals older than 1 year of age, with individuals younger than 1 year classified as pups. Adult individuals are either dominant (the male and female breeding pair) or subordinate (all remaining adults, who act as helpers); dominance is determined through observation of agonistic interactions, scent-marking and grooming (Rasa 1977; Kern and Radford 2013). Individuals are sexed by observation of ano-genital grooming (Kern et al. 2016).

The DMRP maintains a year-round field team of four researchers. Each mongoose group is visited every week for 2–3 days at a time. Typically, an observer arrives at a group's overnight refuge before they wake up in the morning, then follows the group during the day (the day is split into a morning and afternoon observation session) until they settle in the chosen refuge for the night. Observers maintain habituation levels via their continued presence and daily weights sessions; most individuals in the population have been trained to climb into an electronic weighing scale in exchange for a small reward of egg. Individuals are weighed first thing in the morning before they leave their burrow to start foraging, again after the morning foraging session and when they return to their evening refuge (Figure 1.4b). Observers also re-apply dye-marks when they start to fade, track group movement with a GPS, and collect data on group size and composition, individual and group-level behaviours (e.g. sentinel activity, grooming and dominance interactions, nearest-foraging neighbours,

latrine events and intergroup interactions), body mass and life-history events (e.g. pregnancies, births, emigrations, immigrations).

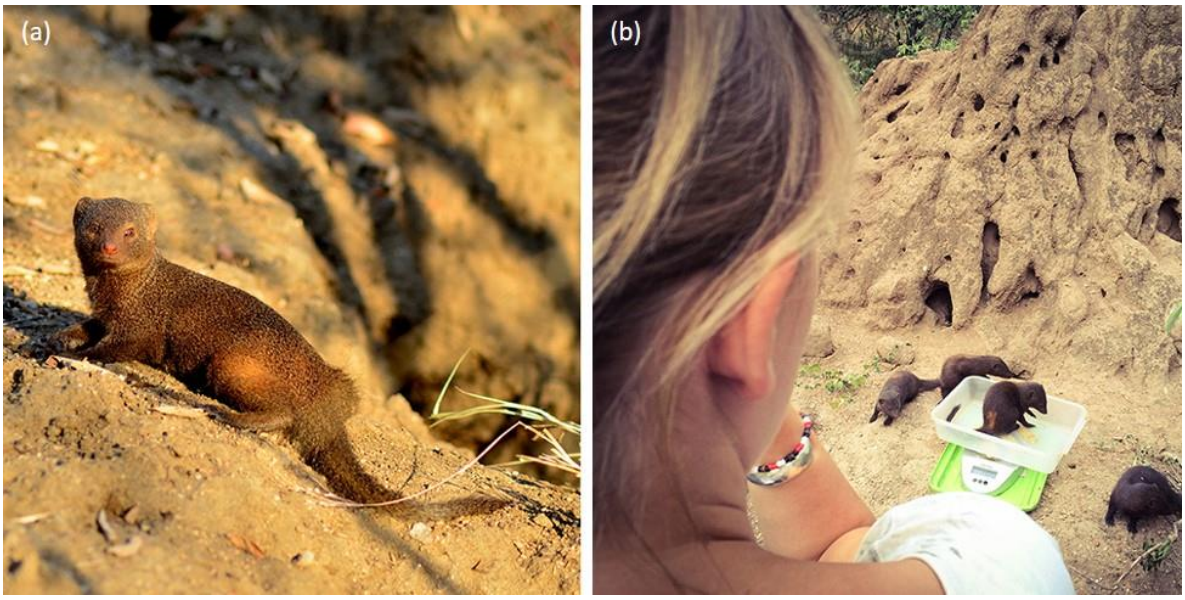

Figure 1.4 A dwarf mongoose with a small left-thigh dye mark on its fur for identification purposes (a), and a morning weights session with a group for the collection of body-mass data (b). Photographs by myself (a) and Martin Aveling (b).

The study was undertaken by permission from the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UIN/17/074).

1.5 Thesis outline

This thesis reports four years of my work both conducting research and co-managing the DMRP (with responsibility, among other things, for selecting and training research assistants, acting as field manager when in South Africa, liaising with the field manager when back in Bristol, trouble-shooting project logistical issues and managing the error-checking of the long-term databases). Combining detailed observations of natural behaviour, sound recordings, field experiments and analysis of long-term behavioural and life-history data, I have investigated various aspects of within-group and between-group conflict in dwarf mongooses. Each of the data chapters are written as stand-alone papers to be understood outside the context of this thesis; they are either published already (Chapter Three: Morris-Drake et al. 2019), or are being prepared for submission (Chapters Two, Four and Five) to peer-reviewed journals. As such, they each include their own specific Introduction and Discussion sections; they are formatted individually (in terms of section order) depending on the relevant journals they are published in or to which they are being targeted for submission. In Chapter Two, I focus on

within-group conflict and ask whether memories of prior agonistic interactions can influence post-contest management with a temporal delay. For Chapter Three, I explore the short-term behavioural consequences of outgroup conflict, investigating effects on within-group interactions, group foraging behaviour and individual decision-making. I then address, in Chapter Four, the longer-term consequences of outgroup conflict, considering whether there are carryover effects on behaviour into the following day and whether there are cumulative effects on behaviour and body mass over the course of a week. In Chapter Five, I assess the influence of contests with rivals on reproductive success, and finally, in Chapter Six, I present a critical summary of all four data chapters and my thoughts about future work in the field of social conflict and evolution.

Chapter 2: Experimental Evidence for Delayed Post-contest Resolution Among Wild Dwarf Mongooses

Morris-Drake A., Kern J. M., Radford A. N. Experimental evidence for delayed post-contest resolution among wild dwarf mongooses. In preparation for submission to *Science Advances*.

Chapter Two is presented as for publication with the Methods appearing at the end of the chapter.

AMD co-designed the study, maintained the habituated study population, conducted the fieldwork, carried out the data analysis, interpreted the results and drafted the manuscript; JMK established and maintained the habituated study population, helped interpret the results and commented on the manuscript; ANR co-designed the study, advised on data analysis, helped interpret the results and commented on the manuscript.

2.1 Abstract

In many species, the costs of within-group conflict are mitigated by subsequent changes in behaviour (e.g. avoidance or increases in affiliation) involving protagonists and bystanders (non-participants). However, the focus has been on the immediate aftermath of contests; despite increasing evidence that nonhuman animals use memories of past events to inform later decision-making, there has been no investigation of delayed conflict resolution. Here, we provide experimental evidence of delayed conflict resolution in wild dwarf mongooses (*Helogale parvula*). First, we used responses to natural foraging displacements and those simulated by call playbacks to demonstrate that bystanders take notice of the vocalisations produced during such within-group conflict; there was no evidence that bystanders engage in immediate post-contest resolution (grooming). We then used a second field-based playback experiment to test for a delayed effect of within-group conflict on grooming interactions. During 3-h afternoon trial sessions, perceived conflict between a dominant aggressor and a subordinate victim was either increased (playback of their foraging-displacement calls) or unmanipulated (playback of their foraging close calls as a control). We found treatment differences in the grooming interactions of bystanders at the evening sleeping refuge. Overall, fewer individuals engaged in grooming on conflict evenings, but those that did spent a greater proportion of time grooming than on control evenings. Subordinate bystanders groomed with the simulated aggressor significantly less on conflict evenings compared to control evenings; this treatment difference was not apparent in grooming interactions with the non-playback dominant. Subordinates also groomed more with one another on conflict evenings, but there was no strong evidence for increased grooming of the simulated victim. We believe our study provides experimental evidence that dwarf mongooses can acoustically obtain information about within-group contests (including protagonist identity), retain that information and use it to inform decisions about conflict resolution with a temporal delay.

2.2 Introduction

Conflicts of interest are common in social species, with disagreements between group members arising over access to mates or food, synchronisation of group activities and the direction of travel (Aureli et al. 2002; Conradt and Roper 2009; Hardy and Briffa 2013). Within-group conflict, especially if it escalates to aggression, can be costly in terms of injury and mortality, time and energy expenditure, increased stress and disrupted social relationships (Aureli 1997; de Waal 2000; Aureli et al. 2002). Conflict management strategies that minimise these costs, either by reducing the likelihood of aggressive escalation (prevention) or by mitigating and repairing the damage arising from such physical contests (resolution), have therefore evolved in many species (Aureli and de Waal 2000; Aureli et al. 2002). Much of the early work on conflict resolution focussed on interactions between the protagonists (the aggressor and the victim): many studies have documented increases in affiliation between former opponents in the aftermath of a contest (reconciliation; de Waal and van Roosmalen 1979; de Waal 2000; Aureli et al. 2002), although there are also examples of victims avoiding aggressors (wariness; Aureli 1992; Kutsukake and Clutton-Brock 2008; Benkada et al. 2020). More recently, attention has shifted to the involvement of bystanders (uninvolved group members) in post-contest behaviour, particularly bystander-initiated affiliation with the victim as a means of self-protection, substitute reconciliation or consolation (Fraser et al. 2008, 2009; Wittig and Boesch 2010; Schino and Marini 2012). There is also some evidence of bystander-initiated affiliation with the aggressor, which could function as appeasement (van Hooff 1967) to reduce the likelihood of renewed aggression (Palagi et al. 2008; Romero et al. 2011; Cordoni and Palagi 2015; Pallante et al. 2018), and group-wide post-contest affiliation among bystanders, perhaps to reduce conflict-induced anxiety (Judge and Mullen 2005; De Marco et al. 2010). However, to the best of our knowledge, this research has focussed solely on behavioural interactions that occur in the immediate aftermath (usually within 10 minutes) of an aggressive interaction; the possibility of delayed conflict resolution has not been explored.

There is increasing experimental evidence that nonhuman animals can remember past events and use information from them when making later social decisions (Seyfarth and Cheney 1984; Carter and Wilkinson 2013; Wittig et al. 2014; Kern and Radford 2018). This includes conflict management, at least with respect to decisions about whether to get involved in an aggressive interaction. For example, baboons (*Papio hamadryas ursinus*) were more likely to move towards playback of a grunt call given to recruit support in an aggressive interaction if they had recently groomed with the caller (Cheney et al. 2010). Similarly, vervet monkeys (*Chlorocebus pygerythrus*) were more likely to offer coalitionary support in a conflict if they had recently groomed together (Borgeaud and Bshary 2015).

Other studies have shown that individuals can use knowledge of previous agonistic interactions to inform how best to respond to further aggression. For instance, chimpanzees (*Pan troglodytes*) that had been involved in an unreconciled conflict reacted aversively to playback of an aggressive bark from their former opponent's bond partner (a third-party individual likely to offer aggressive support to the former opponent; Wittig et al. 2014). Moreover, it was recently shown that bystander wasps (*Polistes fuscatus*) were more aggressive towards individuals that they had observed to be less aggressive in a previous fight with a third party (Tibbetts et al. 2020). It is thus plausible that resolution-related behaviours could also occur some time after the relevant conflict.

To make behavioural decisions, animals obtain information about social interactions using a variety of sensory modalities (Davies et al. 2012). Most research considering social monitoring of within-group conflict has focused on situations where individuals have seen the interaction, hence bystanders are commonly defined as individuals who have observed the encounter (Schino and Sciarretta 2015). But for those species living in visually occluded environments, those where group members can be scattered over large distances or those that forage in a way that prevents simultaneous vigilance, acoustic cues can be a beneficial source of social information (Bradbury and Vehrencamp 2011). Numerous species vocalise during or at the end of within-group contests (Brown et al. 2006; Bertram et al. 2010; Slocombe et al. 2010). For example, chimpanzees and rhesus macaques (*Macaca mulatta*) produce screams whilst experiencing aggression (Gouzoules et al. 1984; Slocombe et al. 2009), whilst little blue penguins (*Eudyptula minor*) give specific calls after a contest is finished (Waas 1990). These vocalisations likely provide bystanders with valuable information about within-group conflict (Gouzoules et al. 1984; Slocombe and Zuberbühler 2007; Szipl et al. 2017; Whitehouse and Meunier 2020). Moreover, they can be used in playbacks to test post-contest behaviour experimentally.

Here, we investigate experimentally the possibility of delayed conflict resolution in a wild population of dwarf mongooses (*Helogale parvula*); the study population has been habituated to close human presence, facilitating detailed observations and field-based manipulations (Kern and Radford 2016, 2017). Dwarf mongooses live in cooperatively breeding groups of up to 30 individuals, comprising a dominant breeding pair (hereafter 'dominant' individuals) and non-breeding subordinate helpers (hereafter 'subordinate' individuals) of both sexes (Rasa 1977). Within-group aggressive interactions take two main forms: relatively rare targeted aggression, which usually acts to reinforce rank and is mainly due to reproductive conflict (Rasa 1977); and relatively common foraging displacements, when a higher-ranking individual displaces a lower-ranking group member from a

foraging patch and steals their prey (Sharpe et al. 2013, 2016). Foraging displacements generally involve the following behavioural sequence: the higher-ranking individual produces deep growls as it approaches the lower-ranking group member; the former then hip-slams the latter away from the food resource; and the displaced individual typically produces high-pitched squeals whilst it retreats (Sharpe et al. 2013, 2016). Previous work has shown that dwarf mongooses can use vocal information to facilitate delayed contingent rewarding of cooperative contributions by groupmates (Kern and Radford 2018). We now test whether group members exhibit delayed responses to vocal cues of within-group conflict.

2.3 Results

We initially used both observational data and a playback experiment to determine whether bystanders take notice of conflict between groupmates and if they engage in affiliative grooming or vocal exchanges in the aftermath (full details in *Methods*). To collect data relating to natural foraging displacements (which occur at a mean±SE rate of 2.6±0.2 events per 3-h observation session, range: 0–10, N=127 observation sessions across eight groups), we conducted focal watches on foraging subordinates in two situations: immediately after the human observer heard a foraging displacement (conflict situation) and on a matched occasion when there had been no foraging displacement for at least 10 min (control situation). Paired data were collected from 16 subordinates in six groups, with conflict and control focal watches counterbalanced in order between individuals. To test experimentally the immediate responses of bystanders, and to isolate the importance of foraging-displacement vocalisations as a cue to conflict occurrence, we presented 17 foraging subordinates in eight groups with two playback treatments in a matched, counterbalanced design (Experiment 1). The conflict treatment entailed playback of close calls from a dominant individual and a subordinate individual from the same group as the focal individual, followed by the dominant growling and the subordinate squealing (simulating a foraging displacement); the control treatment entailed the playback of close calls from the same two individuals for the same duration (40 s) as a full conflict-treatment playback track (Figure 2.1). We chose the combination of a dominant individual as the aggressor and a subordinate individual as a victim for playback because this is the most common dyadic pairing observed in natural foraging displacements (74.3% of 740 events in 12 groups).

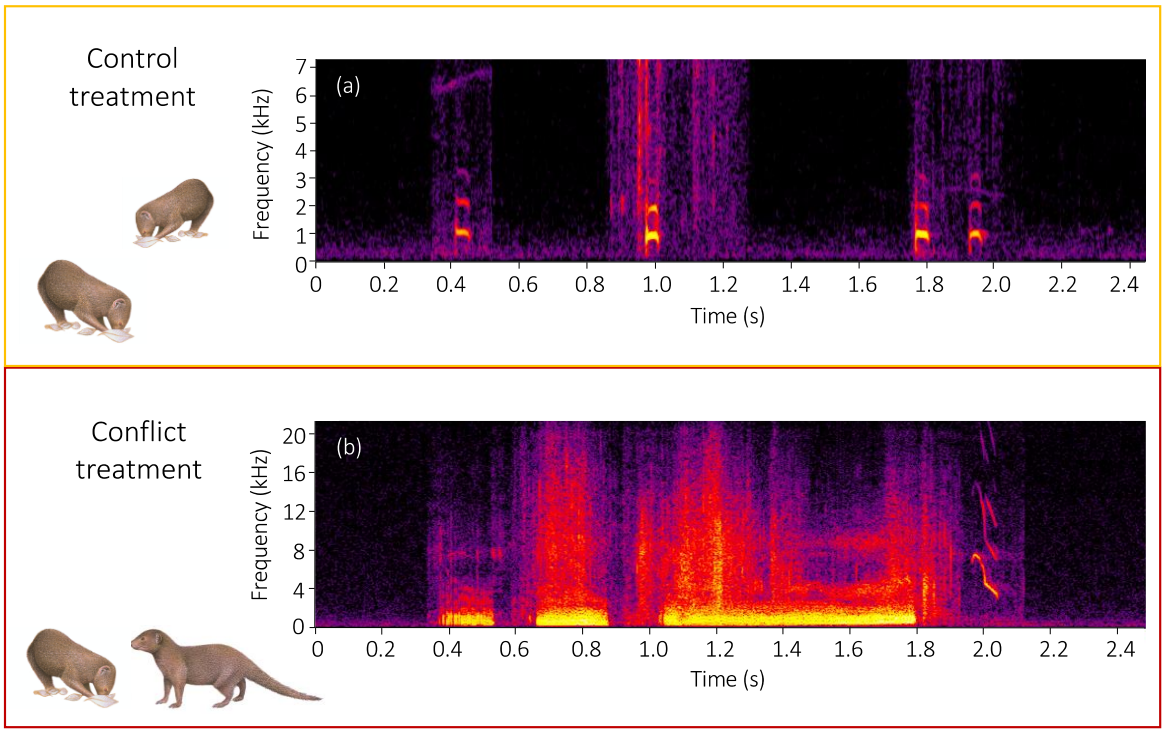

Figure 2.1 Spectrograms of the final sections of control and conflict playback tracks. Control tracks concluded with three close calls from the dominant aggressor followed by one close call from the subordinate victim (a), whilst conflict tracks concluded with three growls from the same dominant aggressor followed by a squeal from the same subordinate victim (b). Spectrograms were created in Raven Pro 1.5 using a 1024 point fast Fourier Transform (Hamming window, 75% overlap, 2.70 ms time resolution, 43 Hz frequency resolution).

We found evidence that bystanders take notice of conflicts between groupmates but no indication of immediate post-conflict affiliative exchanges with either the protagonists or other group members. In the 2–3 min following both natural foraging displacements (Wilcoxon signed-rank test: $Z=3.154$, $N=16$, $P<0.001$; Figure 2.2a) and those simulated by playback ($Z=3.527$, $N=17$, $P<0.001$; Figure 2.2b), focal foragers spent a significantly greater proportion of time vigilant than in matched-control, non-conflict situations. This was because individuals were conducting vigilance bouts both at a significantly greater rate (observational data: $Z=2.517$, $N=16$, $P=0.008$; Figure 2.2c; experimental data: $Z=3.479$, $N=17$, $P<0.001$; Figure 2.2d) and for significantly longer durations (observational: $Z=2.500$, $N=15$, $P=0.009$; Figure 2.2e; experimental: $Z=3.574$, $N=17$, $P<0.001$; Figure 2.2f) in the aftermath of a foraging displacement compared to control periods. However, the focal individual did not engage in any post-conflict grooming in the 5 min following either natural or simulated foraging displacements; grooming is generally rare during foraging periods in dwarf mongooses (90% of grooming bouts occur at the sleeping refuge, N=6,376 bouts, 174 individuals; Kern and Radford 2018).

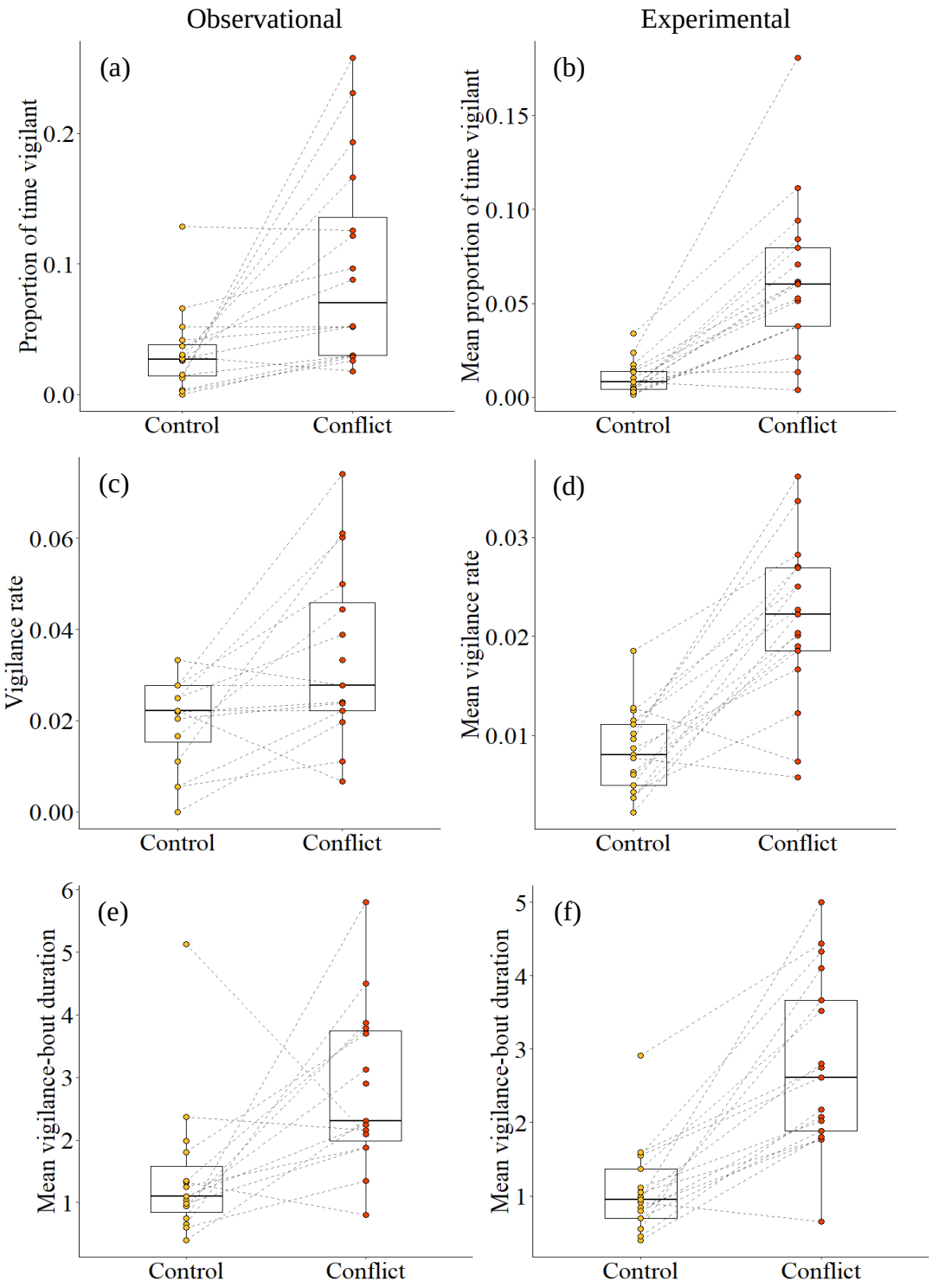

Figure 2.2 Effect of natural foraging displacements (observational) and simulated foraging displacements (experimental) on the vigilance of foraging dwarf mongooses (observational: N=16 individuals in six groups; experimental: N=17 individuals in eight groups). Individuals exhibited an increase in the proportion of time spent vigilant (a,b), rate of vigilance bouts (c,d) and mean duration (s) of vigilance bouts (e,f) following within-group conflict compared to a control situation. Shown in all panels are boxplots with the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range. In all panels, values for each individual are shown separately (yellow=control, red=conflict), with dashed grey lines connecting data from the same individuals.

There was also no evidence of vocal 'grooming-at-a-distance' (Arlet et al. 2015; Kulahci et al. 2015), as the close-call rate of focal individuals was not significantly greater following natural ($Z=1.500$, $N=16$, $P=0.144$) or simulated ($Z=1.491$, $N=17$, $P=0.144$) foraging displacements compared to control situations. The increased vigilance following foraging displacements indicates that other group members have noticed their occurrence; the experimental results demonstrate that the vocal cues are sufficient to trigger this reaction. However, unlike in many primates (Wittig and Boesch 2003; McFarland and Majolo 2012; Palagi et al. 2014) and other species (Seed et al. 2007; Cools et al. 2008; Baan et al. 2014; Yamamoto et al. 2020), there is no evidence that bystanders engage in post-contest affiliative behaviour in the immediate aftermath.

To test if there were delayed effects of within-group conflict on affiliative behaviour (grooming), we conducted a second repeated-measures playback experiment on eight groups (Experiment 2, Figure 2.3; full details in *Methods*). The general experimental design followed Kern and Radford (2018). In each field-based trial session, we either simulated an increase in the conflict between a dominant (aggressor) and a subordinate (victim) group member through playback of their foraging-displacement vocalisations (conflict treatment) or played back just the close calls of those individuals for an equivalent period (control treatment); individual playbacks were as in Experiment 1. Trials were on separate days with treatment order counterbalanced between groups. In each trial, 6–9 playbacks (mean±SE: 8.5±0.2, N=16 trials) were carried out over the course of 3 h in the afternoon whilst the group were foraging and before they moved towards their evening sleeping refuge (mean±SE period between final playback and first grooming bout at the sleeping refuge: 37±5 min, N=16 trials). At the refuge, we collected data *ad libitum* on all adult grooming interactions, including the identity of the individuals involved and bout duration. If within-group conflict does have delayed effects on affiliative behaviour, we expected an increase in the occurrence of foraging displacements to result in changes in grooming levels.

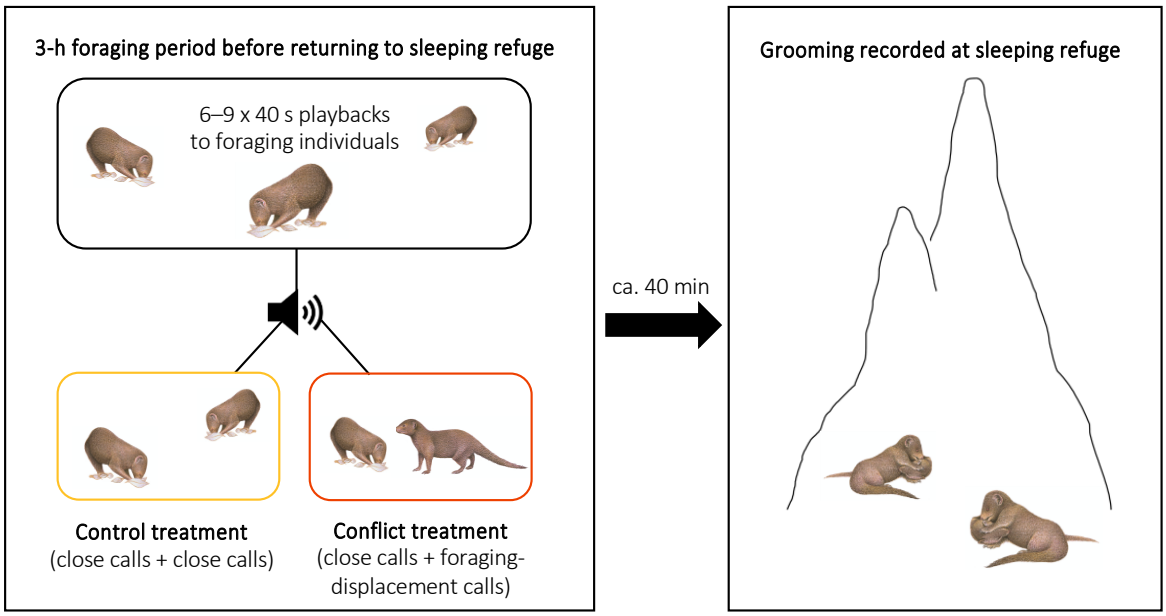

Figure 2.3 Illustration of the protocol for Experiment 2. Additional within-group conflicts between a dominant aggressor and a subordinate victim were simulated during conflict afternoons using playback of foraging-displacement calls, with only close calls of the same individuals played back in control sessions. Grooming at the evening sleeping refuge was subsequently recorded.

Overall, we found that group members were significantly less likely to be involved in grooming interactions in the evenings following conflict afternoons compared to control afternoons (generalised linear mixed model (GLMM): χ^2=5.401, df=1, P=0.020; Table 2.1a; Figure 2.4a). However, when considering only those individuals that engaged in grooming, they spent a significantly greater proportion of time doing so on evenings when there had been an earlier simulated increase in conflict compared to control evenings (linear mixed model (LMM): χ^2=16.522, df=1, P<0.001; Table 2.1b; Figure 2.4b). This was because these individuals were grooming more frequently (χ^2=14.810, df=1, P<0.001; Table 2.1c; Figure 2.4c) and for longer per bout (χ^2=3.958, df=1, P=0.047; Table 2.1d; Figure 2.4d) after a simulated increase in conflict compared to control conditions. These results indicate that there is an overall response to simulated conflict within the group, but we also made some specific predictions. Assuming that aggressors and victims can be identified from their vocalisations—which has been demonstrated for dwarf mongoose close calls (Sharpe et al. 2013), recruitment calls (Kern and Radford 2016; Rubow et al. 2017*a*) and surveillance calls (Kern and Radford 2018)—we predicted that subordinates might engage in either less grooming (due to wariness) or more grooming (as possible appeasement) with aggressors, and that they might engage in more grooming with victims (as possible consolation).

Table 2.1 Output from a GLMM (a) and LMMs (b–d) investigating the grooming behaviour of adult individuals at the evening refuge. All models contained treatment as a fixed effect, with Individual ID nested within Group ID as random effects. The GLMM (binomial error distribution and logit-link function) examined whether an individual was involved in a grooming bout (Yes or No). Subsequent LMMs focused on those individuals that did participate in grooming, examining the log-transformed proportion of time spent grooming (b), the log-transformed rate of grooming interactions (c) and the log-transformed mean grooming-bout duration (d). Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Likelihood of grooming occurrence					
Random effects	*Group ID*	0.959			
	Individual ID in Group ID	<0.001			
Minimal model	(Intercept)	1.267±0.497			
	Treatment	**1.106±0.488**	**1**	**5.401**	**0.020**
(b) Proportion of time spent grooming					
Random effects	*Group ID*	0.360			
	Individual ID in Group ID	0.555			
Minimal model	(Intercept)	-2.114±0.186			
	Treatment	**-0.681±0.155**	**1**	**16.522**	**<0.001**
(c) Rate of grooming bouts					
Random effects	*Group ID*	0.262			
	Individual ID in Group ID	0.353			
Minimal model	(Intercept)	-1.269±0.139			
	Treatment	**-0.515±0.125**	**1**	**14.810**	**<0.001**
(d) Mean grooming-bout duration					
Random effects	*Group ID*	0.217			
	Individual ID in Group ID	0.258			
Minimal model	(Intercept)	3.257±0.104			
	Treatment	**-0.167±0.083**	**1**	**3.958**	**0.047**

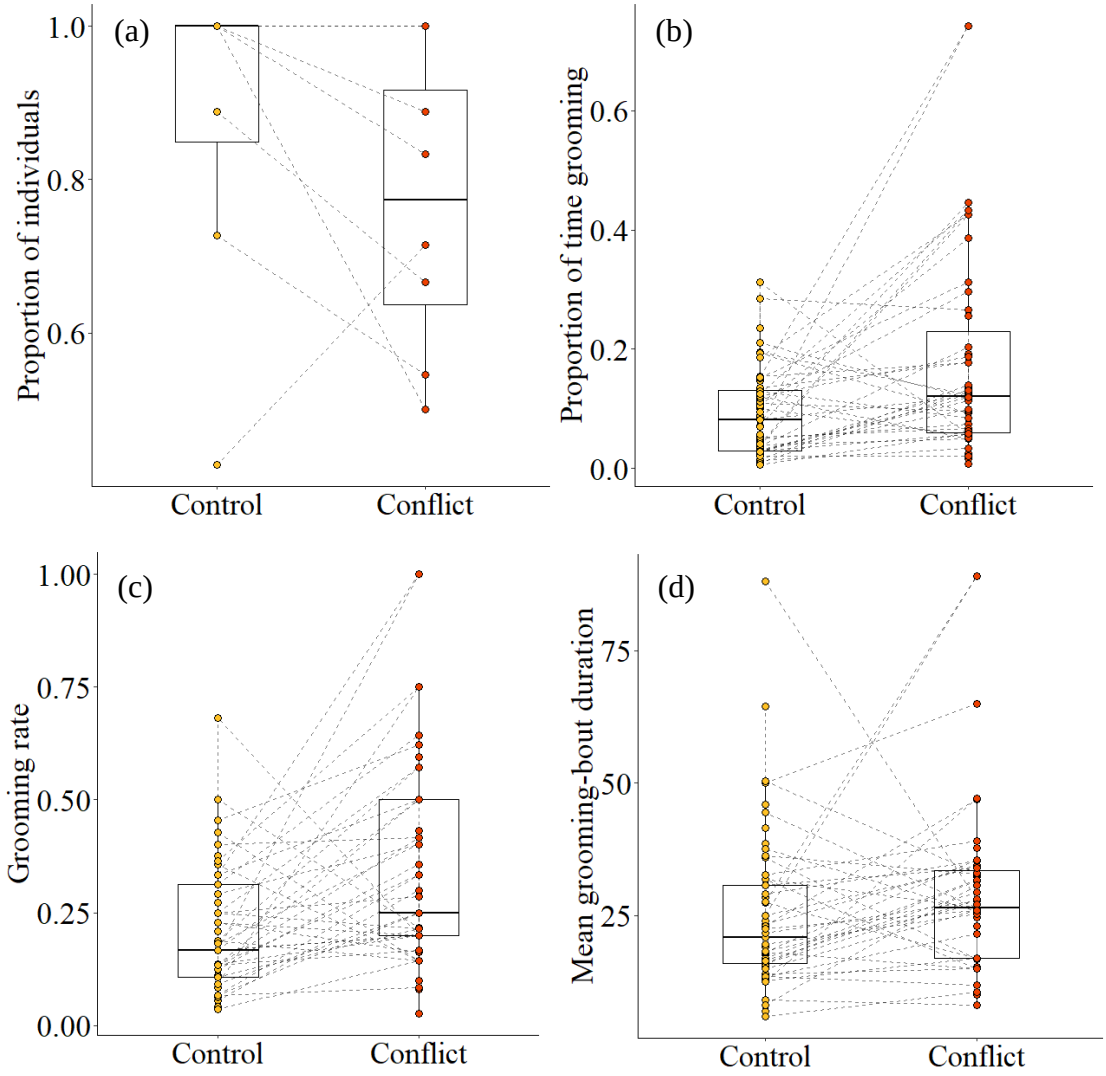

Figure 2.4 Delayed effects of experimentally increased within-group conflict on the grooming behaviour of dwarf mongooses. Fewer adult individuals engaged in evening grooming behaviour after conflict afternoons compared to control afternoons (a). But those individuals that groomed, did so for a greater proportion of time (b), at a greater rate (c) and for longer mean bout durations (d) on conflict compared to control evenings. Shown in (a) is the proportion of individuals that engaged in grooming for each group (N=8) in each treatment. Shown in (b)–(d) are values for each individual separately (yellow=control, red=conflict), with dashed grey lines connecting data from the same individuals; orphan points, where an individual only groomed in one treatment type, are also plotted; N=104 observations from 63 individuals in eight groups. Shown in all cases are boxplots with the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range.

We found strong evidence that simulating aggressive behaviour by a dominant individual during the afternoon resulted in subordinates engaging in less grooming with it at the sleeping refuge that evening. Following conflict trials, subordinates groomed with the dominant pair for a smaller proportion of time than after control trials (Wilcoxon signed-rank test: Z=2.240, N=8, P=0.021; Figure 2.5a). This reduced affiliative engagement by subordinates was driven by a change in behaviour

towards the simulated aggressor specifically. Whilst there was no significant treatment difference in the proportion of time that subordinates groomed with the dominant whose calls were not played back (Z=0.105, N=8, P=1; Figure 2.5b), there was significantly less grooming between subordinates and the simulated aggressor on conflict evenings compared to control evenings (Z=2.521, N=8, P=0.008; Figure 2.5c). At least in part, this difference in grooming with the two dominants was due to the number of subordinates engaging with them: whilst there was no significant treatment difference in the proportion of subordinates that groomed with the non-playback dominant (Z=0.813, N=8, P=0.499; Figure 2.5d), a significantly smaller proportion of subordinates groomed with the simulated aggressor in the evening of conflict trials compared to control trials (Z=2.201, N=8, P=0.033; Figure 2.5e). Moreover, on those occasions where individuals did groom, bout durations were somewhat shorter on conflict evenings compared to control evenings for grooming involving simulated aggressors (mean±SE duration, post-control: 34±11 s; post-conflict: 23±5 s; N=4 pairs of trials), while the reverse was true for grooming involving the matched dominant (post-control: 28±8 s; post-conflict: 34±8 s; N=4 pairs of trials); small sample sizes precluded statistical analysis.

If hearing within-group conflict led to a general change in behaviour, we would expect the grooming that subordinates engaged in with the aggressor and the non-playback dominant to be similarly affected. However, we found a reduction in grooming with the aggressor only, a result which also demonstrates that aggressors can be identified from vocal cues alone. Some studies have documented increased grooming of aggressors by bystanders in the immediate aftermath of a contest (Palagi et al. 2008; Romero et al. 2011; Cordoni and Palagi 2015; Pallante et al. 2018), whilst a few others have not found any evidence for such an increase (Judge 1991; Verbeek and de Waal 1997; Romero et al. 2008). To our knowledge, this is the first evidence for a reduction in grooming of aggressors by bystanders. Subordinate bystanders could be avoiding the aggressor to reduce the likelihood of redirected aggression, which parallels the main strategy employed in the immediate aftermath of contests by meerkat (*Suricata suricatta*) and rook (*Corvus frugilegus*) victims (Kutsukake and Clutton-Brock 2008; Benkada et al. 2020) and adds to the evidence that avoidance is a commonly used conflict-resolution strategy in hierarchical species (Sommer et al. 2002; Kutsukake and Clutton-Brock 2008).

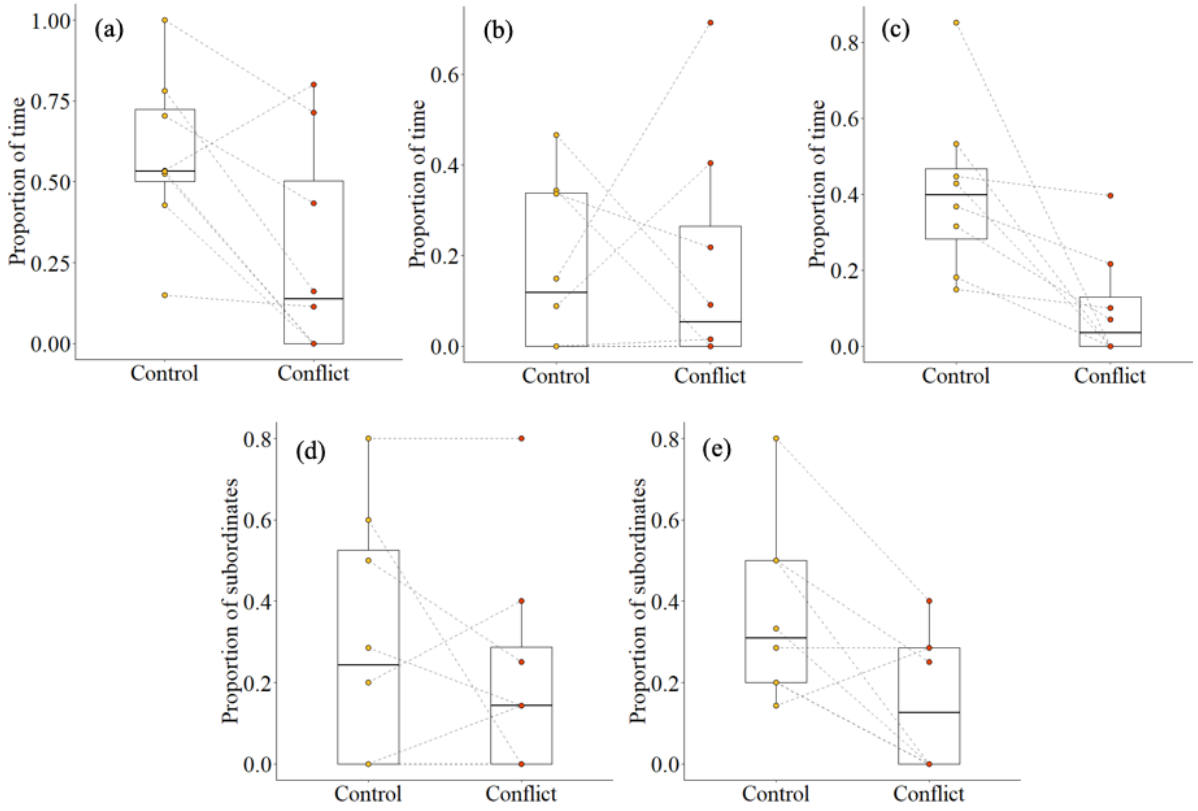

Figure 2.5 Simulated within-group conflict between a dominant aggressor and a subordinate victim during the afternoon led to changes in the grooming behaviour of bystanders with dominants at the evening sleeping refuge. The proportion of time that subordinates and dominants groomed was reduced on conflict evenings (a); a result not driven by the proportion of time that subordinates and non-playback dominants groomed (b), but instead by a reduction in the proportion of time that subordinates and aggressors groomed (c). The proportion of subordinates involved in grooming interactions with non-playback dominants did not differ between treatments (d) but that with aggressors was lower on conflict evenings compared to control evenings (e). Shown in all panels are boxplots with the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range. Values for each group (N=8) are plotted separately (yellow=control, red=conflict), with dashed grey lines connecting data from the same groups. In some instances, more than one group has the same value, hence the number of dashed lines can appear less than eight.

We also found some evidence that increasing within-group conflict during the afternoon resulted in increased evening grooming between subordinates. When considering bouts between all subordinates, there was no significant treatment difference in the proportion of time spent grooming (Wilcoxon signed-rank test: Z=1.540, N=8, P=0.146), but subordinate–subordinate grooming bouts were, on average, significantly longer on conflict evenings compared to control evenings (Z=2.366, N=7, P=0.015; Figure 2.6a). Considering bouts involving particular individuals, there were indications that victims might receive a conflict-driven increase in grooming from other subordinates not seen for preselected control subordinates (those whose squeals had not been played back), but no statistically significant differences. The proportion of time grooming that involved the simulated victim was

doubled on conflict evenings (mean±SE: 0.31±0.09) compared to control evenings (0.15±0.06; Z=1.572, N=8, P=0.156; Figure 2.6b), whereas there was no such increase for the preselected control subordinate (conflict: 0.28±0.09; control: 0.37±0.12; Z=0.280, N=8, P=0.843; Figure 2.6c). The treatment difference in mean bout duration was greater for grooming involving simulated victims (36±14 s, N=3 pairs of trials) than that involving preselected control subordinates (22±24 s, N=3 pairs of trials), but too few matched evenings involved the relevant individuals to allow statistical testing. The increase in the average duration of subordinate–subordinate grooming is in-line with the increase in bystander–bystander grooming seen in some species in the immediate aftermath of a contest (Judge and Mullen 2005). Such affiliation could reduce the group-wide social anxiety induced by aggression (De Marco et al. 2010; Judge and Bachmann 2013; Schino and Sciarretta 2015).

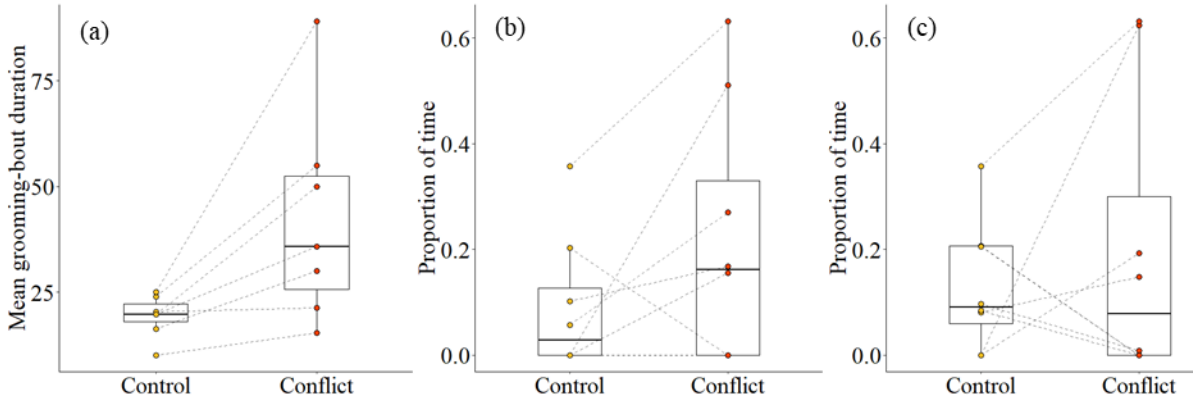

Figure 2.6 Simulated within-group conflict between a dominant aggressor and a subordinate victim during the afternoon led to changes in the grooming behaviour between subordinates at the evening sleeping refuge. Considering all subordinates, the mean duration (s) of grooming bouts between was greater on conflict evenings compared to control evenings (a). There was an indication that other subordinates groomed with victims for a greater proportion of time on conflict evenings, although the result was not statistically significant (b), but no equivalent treatment difference in the proportion of time that subordinates groomed with non-victim subordinates (c). Shown in all cases are boxplots with the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range. Values for each group (N=8) are plotted separately (yellow=control, red=conflict), with dashed grey lines connecting data from the same groups. In some instances, more than one group has the same value, hence the number of dashed lines can appear less than eight.

2.4 Discussion

We believe that we provide compelling experimental evidence for delayed post-contest resolution. Dwarf mongoose bystanders did not engage in any obvious post-contest affiliation in the immediate aftermath of simulated foraging displacements involving a dominant and subordinate group member, but did adjust their later grooming behaviour at the evening sleeping refuge following an afternoon of increased within-group conflict. Numerous studies on a range of species have found changes in

affiliative behaviour between various combinations of protagonists and bystanders in the minutes after within-group contests (de Waal 2000; Aureli et al. 2002). It remains unknown whether there might be delayed effects of those contests that are not resolved immediately in these species. By using call playbacks, we likely did not alter the state or behaviour of the individuals who were simulated to be the aggressor and victim. Consequently, we can rule out the possibility that differences in grooming result from experimentally induced satiation effects (which might have been the case if we had caused foraging displacements with the presentation of food items; Sharpe 2013). Moreover, our experimental design allows us to conclude that the delayed grooming effects are most likely driven by subordinate bystanders behaving differently towards aggressors (and potentially the victims), rather than solicitation or rejection of grooming by simulated protagonists. Overall, our results demonstrate that individuals can retain information relating to earlier within-group conflict and use it when making later decisions about resolution-related behaviours.

Our experiments show that dwarf mongooses can extract information about within-group conflict, and the identity of at least some protagonists, from vocal cues alone. This adds to a growing body of work demonstrating the ability of social species to garner information acoustically about aggressive interactions (Gouzoules et al. 1984; Slocombe and Zuberbühler 2007; Slocombe et al. 2009, 2010); for example, male little blue penguins had an increased heart rate after hearing vocalisations produced by winners of a contest compared to those produced by losers (Mouterde et al. 2012). Our findings also complement the small number of studies showing that social animals use vocalisations to assess the behaviour, such as the reliability (Blumstein et al. 2004) and cooperative contributions (Kern and Radford 2018), of individually identifiable groupmates. Acoustic monitoring is beneficial as it allows information acquisition in environments where it would be difficult to do so visually (e.g. in low-light and dense vegetation) or when group members are widely scattered and communication is needed over long distances (Bradbury and Vehrencamp 2011). Moreover, acoustic information can be gathered at a relatively low cost: it can be done whilst still actively foraging (Hollén et al. 2008) and, in the case of aggressive encounters, at a safe distance that minimises the risk of the information-gatherer receiving any redirected aggression. Monitoring behaviours this way is likely not possible for all within-group interactions (e.g. grooming) or in all social systems, but the calls commonly produced during and at the end of aggressive interactions (Silk et al. 1996; Brown et al. 2006; Bertram et al. 2010; Slocombe et al. 2010) provide a valuable means for bystanders to inform subsequent decision-making.

We found strong evidence that subordinate bystanders engage in less grooming with simulated aggressors, but whether they increased their grooming with the simulated victim was less clear-cut. There are several possible explanations for this difference in the strength of response exhibited to the two protagonists. First, all subordinates might be wary of the aggressor and so potentially reduce their grooming with that individual, whereas perhaps only those who are strongly bonded to the victim might engage in grooming with it (Fraser et al. 2008, 2009; Romero and de Waal 2010); any such victim-related effect might be diluted by considering all subordinates in analyses. Strong within-group relationships are apparent in dwarf mongoose groups (Kern and Radford 2016, in revision), but we do not have the power in this study to consider how relationship quality influences delayed post-contest grooming. Another possible reason for the difference in grooming responses to aggressors and victims is that there could be selective attention towards high-ranking individuals (Chance 1967; Keverne et al. 1978; McNelis and Boatright-Horowitz 1998; Deaner et al. 2005; Grampp et al. 2019). Many primate species, for example, focus attention on higher-ranking groupmates or those with whom they have an antagonistic relationship, possibly to avoid aggression (Schino and Sciarretta 2016). Since our simulated aggressors were dominants and our simulated victims were subordinates, the stronger effect of increased conflict on grooming with the former could reflect such an attention bias. Alternatively, our results could be driven by differences in the natural acoustic properties of aggressive growls and submissive squeals. In principle, squeals might encode less identity information than growls (Rendall et al. 1996; Owren and Rendall 2003), although a number of studies have found that calls similar in structure to dwarf mongoose squeals are individually identifiable (Cheney and Seyfarth 1980; Gouzoules et al. 1984; Fischer 2004; Slocombe and Zuberbühler 2005; Fugate et al. 2008). In addition, our playback contained three growls and one squeal (to reflect natural foraging displacements), which could have aided easier discrimination of the aggressor compared to the victim. It might also be more cognitively demanding for receivers to discriminate the squeals from multiple subordinate individuals in a group, compared to growls, which are highly likely to come from one of the two dominant individuals. Finally, since contest-related vocalisations may vary depending on the severity of an attack (Gouzoules et al. 1984; Slocombe and Zuberbühler 2007; Slocombe et al. 2009), it is possible that we used less salient squeals than growls in our playbacks. Future work is required to tease these possibilities apart.

In summary, our results suggest that dwarf mongooses can obtain information about within-group contests (including protagonist identity) acoustically, retain that information and use it to inform decisions about conflict resolution with a temporal delay. There is increasing experimental evidence that social animals can remember past events and take these into account when deciding

whether to get involved in a contest (Cheney et al. 2010; Wittig et al. 2014; Borgeaud and Bshary 2015; Tibbetts et al. 2020); we demonstrate that this ability extends to conflict resolution. The cognitive demands of tracking individuals and their behaviours, remembering that information and using it when making decisions is why social interactions within (Dunbar and Shultz 2007) and between (Ashton et al. 2020) groups are believed to be strong drivers of animal intelligence.

2.5 Methods

2.5.1 Study Site and Population

We conducted our study on Sorabi Rock Lodge (24° 11'S, 30° 46'E), a private game reserve in the Limpopo Province, South Africa; full details available in Kern and Radford 2013. This is the site of the Dwarf Mongoose Research Project (DMRP), which has been studying a wild population of dwarf mongooses since 2011. At the time of study (June to October 2019; non-breeding season), eight dwarf mongoose groups (mean±SE group size: 12.3±1.7, range: 5–16) were fully habituated to human observers on foot (<5 m). All the individuals in the population were identifiable, either through dye-marks on their fur (blond hair dye applied using an elongated paintbrush) or natural features, such as scars. Individuals younger than 1 year were classified as pups and those older than 1 year were classified as adults (Kern et al. 2016); data collection focused on adults as pups are seldom involved in foraging displacements. Adults were sexed by observing ano-genital grooming (Kern et al. 2016) and classified as either dominants (the male and female breeding pair) or subordinates (Kern and Radford 2013, 2014); dominance status was established through observation of targeted aggression, scent-marking and reproductive behaviour (Rasa 1977; Kern and Radford 2013).

2.5.2 Observational Data Collection

To determine the natural frequency of foraging displacements over our experimental period, we recorded all detected occurrences of such behaviour during observation sessions; this included displacements that were seen and heard. The calculated rate is likely a conservative estimate as an observer could have missed hearing a foraging displacement (particularly when group members were foraging far apart). We used data collected *ad libitum* as part of the long-term DMRP to assess the likelihood of particular dyads of individuals (aggressor–victim: dominant–dominant, dominant–subordinate, subordinate–subordinate, subordinate–dominant) being involved in a foraging displacement.

To collect data on responses to natural foraging displacements, we conducted paired focal watches (conflict and control) of 2–3 min duration on 16 subordinate group members in six groups

whilst they were foraging; conflict and control focal watches did not differ significantly in their duration (Wilcoxon signed-rank test: Z=0.952, N=16, P=0.380). A conflict watch was carried out immediately after a foraging displacement was heard by the observer, whilst a control watch was carried out when there had been no detected foraging displacement (or any other agonistic interaction) for at least 10 min. We only carried out focal watches when the relevant mongoose was in medium-cover habitat (20−60% ground cover), weather conditions were calm (still or light breeze), there had been no alarm call (conspecific or heterospecific) in the previous 10 min, there had been no predator encounter or intergroup interaction for at least 30 min, and the focal individual was not on the periphery of the group. We abandoned focal watches, and repeated them later, if the focal individual stopped foraging or if there was an alarm call within the first 2 min. Otherwise, we aimed to collect 3 min of uninterrupted data, but if a behavioural change or alarm call occurred between the second and third minute, then the focal watch was retained. Pairs of watches on the same focal individual were completed within 1 month (mean±SE: 8.1±2.7 days apart, range: 0–30 days); group composition always remained the same between a pair of watches, and a minimum of 1 h was left between watches that were conducted on the same day. We watched nine individuals first in control conditions and seven first following a foraging displacement.

During each focal watch, we recorded behavioural data to a Dictaphone (ICD-PX312, Sony, Sony Europe Limited, Surrey, UK). Dwarf mongooses have two types of vigilance behaviour: vigilance scans, where individuals stop foraging from a head-down position to scan their surroundings (Kern et al. 2016, Morris-Drake et al. 2016); and sentinel behaviour, where individuals scan from a raised position (minimum 10 cm above ground level; Kern and Radford 2013, 2014). They also produce low-amplitude close calls continuously whilst foraging (Kern and Radford 2013; Sharpe et al. 2013). Throughout each focal watch, we dictated the start and end point of each vigilance scan and sentinel bout, along with the occurrence of each close call and any grooming interaction with a groupmate. No grooming occurred during these focal watches. These data were used to calculate the proportion of time spent vigilant and the close-call rate. On finding a significant increase in the proportion of time vigilant (see *Results*), we analysed the vigilance rate and mean duration of vigilance bouts to understand what was driving the increase; this hierarchical approach avoids the inflation of Type I errors. No grooming occurred during these focal watches and no individuals acted as a sentinel during the observational focal watches and therefore the above response measures relating to vigilance were based on scan data only. We used Wilcoxon signed-ranks tests to analyse the dependent variables in SPSS 24 (IBM Corp, 2016); due to small sample sizes, we used the Monte Carlo resampling method (based on 10,000 samples) to generate P-values.

2.5.3 Experimental Stimuli

We conducted two field-based repeated-measures experiments using playbacks to simulate the occurrence of conflict between group members. Each experiment involved the playback of 'conflict' and 'control' tracks. We recorded all calls for track creation when weather conditions were calm using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ) connected to a handheld Sennheiser ME66 directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). The Marantz was set to record at 48 kHz with a 16-bit resolution, and files were saved in wav format. For conflict tracks, we recorded aggressive growls and submissive squeals opportunistically from natural foraging displacements or from conflicts induced by the presentation of a small amount of hard-boiled egg. Growls were recorded from either the dominant male or dominant female in each group and squeals were recorded from a subordinate male or female in each group; all recorded calls came from foraging displacements where the dominant was the aggressor and the subordinate was the victim. We recorded close calls, for use in both control and conflict tracks, from the same dominant and subordinate individuals whilst they were foraging. Recordings of all vocalisations were made 0.5–5 m from the relevant individual.

We formed 40 s playback tracks in Audacity (version 2.1.3) by extracting calls of good signal-to-noise ratio from original recordings and inserting them into ambient-sound recordings; ambient sound was recorded from the centre of the territory of the focal group on calm days and in the absence of dwarf mongooses. The first 36 s of each track (conflict and control) consisted of close calls from the relevant dominant and subordinate individual, with a rate of 1 close call every 6 seconds per individual. This rate of close calling falls within the natural range (Kern and Radford 2013). For conflict tracks, the last 4 s consisted of a sequence of three growls from the dominant followed by one squeal from the subordinate; multiple growls and a single squeal reflects natural foraging displacements (personal observation). In control tracks, the last 4 s consisted of three close calls from the dominant followed by one close call from the subordinate, to match the number of vocalisations in conflict tracks. Tracks always contained vocalisations from same-sex individuals.

We created nine unique conflict and control tracks for each group. Given that the first 36 s of each track comprised close calls from the dominant and subordinate individual, we created three close-call sequences for each individual (each sequence contained six close calls), resulting in nine unique close-call combinations. For the conflict tracks, in which the last 4 s contained growls and a squeal, we created three different growl sequences for the dominant (each sequence consisted of

three growls), which were combined with three separate squeals from the subordinate. Lastly, for the final 4 s of the control tracks, we made three close-call sequences for the dominant (each sequence contained three close calls to match the number of growls in conflict tracks), and combined these with three different close calls from the subordinate. We applied a low-pass filter (set to 200 Hz) to all tracks to remove low-frequency disturbance.

We played back tracks from an iPhone (Apple, Cupertino, CA), connected to a Rokono B10 (London, UK) portable loudspeaker concealed in vegetation. We set the amplitude to a sound-pressure level of 55 dB(A) at 1 m for close calls and growls, and 65 dB(A) at 1 m for squeals. This was the relevant volume of these vocalisations as determined by measurement of natural calls with a HandyMAN TEK 1345 sound-level meter (Metrel UK Ltd., Normanton, UK).

2.5.4 Experiment 1 Protocol

Experiment 1 was a complement to the observational focal watches (see *Observational Data Collection*), aiming to test whether bystanders could garner information about within-group conflict solely from vocalisations. We randomly selected 17 subordinate individuals (excluding those used in the playbacks) to receive the two treatments (conflict and control) on separate days and in a counterbalanced order. Each treatment was repeated 2–3 times per individual during the same observation session, using a different playback track each time, with a minimum of 10 min between repeats; for one individual, it was possible to run one of the treatments only once. We completed the two treatments for the same individual within 2 weeks of each other (mean±SE: 2.8±0.7 days apart, range: 1–11 days) and at the same time of day (either between 07:00 and 12:00 or between 12:30 and 17:30). The 17 focal individuals were from eight groups; for groups where there was more than one focal individual (N=4 groups), we completed both treatments on one individual before moving on to the next.

We conducted playbacks when the focal individual was foraging in medium habitat with little or no breeze and when the callers in the playback were not the focal individual's nearest neighbour (other pre-requisites detailed in *Observational Data Collection*). Where possible, we placed the loudspeaker in the general direction of the playback individuals. As soon as the playback finished, we conducted a 2–3 min focal watch; the mean duration of focal watches was not significantly different between treatments (Wilcoxon signed-rank test: Z=1.397, N=17, P=0.168). Collection of vigilance and close-calling data was identical to that for observational focal watches.

We analysed the same response variables as those for the natural foraging displacements (see *Observational Data Collection*): proportion of time spent vigilant, vigilance rate, mean duration of vigilance bouts and the close-call rate; no grooming occurred in any focal watches. We used the same hierarchical approach to analyse the vigilance response measures as with the equivalent observational data. Since each treatment was repeated 2–3 times on an individual, we analysed the mean for each response measure; Wilcoxon signed-ranks tests were used. In five out of 94 trials, an individual acted as a sentinel. We therefore ran the vigilance response measures including and excluding this sentinel behaviour. The data reported in the *Results* section are those excluding sentinel bouts, but qualitatively similar results were found for those including this behaviour.

2.5.5 Experiment 2 Protocol

Experiment 2 aimed to test whether there was a delayed effect of within-group conflict on affiliation between group members. We gave eight groups two treatments each on separate days, with treatment order counterbalanced between the groups. On conflict days, the perceived level of within-group conflict was increased during the afternoon by playback of up to nine conflict tracks. On control days, perceived levels of within-group conflict were unmanipulated; up to nine control tracks were played back during the afternoon instead. There was no treatment difference in the number of natural foraging displacements that occurred throughout the afternoon (Wilcoxon signed-rank test: Z=1.725, N=8, P=0.158). We completed the two treatments to the same group within 2 weeks of each other (mean±SE: 3.3±1.0 days apart, range: 1–9 days). Trials were only attempted when the weather conditions were suitable (not too windy or cold) and were abandoned if any major disturbances occurred during the afternoon (e.g. predation attempts, intergroup interactions, multiple latrine events).

On a trial afternoon, we played back tracks from the centre of the foraging group approximately every 20 min during the 3-h period before the group started moving to an evening sleeping refuge. There were five trials (two conflict, three control) where adverse conditions (e.g. groups on the move, individuals foraging too far apart) prevented us from completing all nine planned playbacks in an afternoon (mean±SE number of playbacks: 8.5±0.2, range: 6–9) before the group headed to their sleeping refuge. Once at the refuge (always termite mounds), we recorded all instances of adult grooming behaviour *ad libitum* until the mongooses went below ground for the night. This involved dictating the identity of grooming partners and the start and end point of each bout. Periods of grooming data collection at the refuge (mean±SE: 15.5±2.3 min, range: 2–37 min)

were not significantly different in duration between treatments (Wilcoxon signed-rank test: Z=1.332, N=8, P=0.209).

To analyse the overall grooming data at the refuge, we constructed mixed models in RStudio 3.6.2 (R Core Team 2019) using the package lme4 (Bates et al. 2015). For all models, we included treatment as a fixed effect and nested Individual ID within Group ID as random effects to account for data from the same individuals and groups. Error distributions were chosen such that there were no deviations from normality or homoscedasticity, as checked by graphical examination of residual plots. Since we only had one fixed effect, to assess the significance of treatment on the dependent variables, we compared a model containing our fixed effect to a model without it (null model) using a likelihood ratio test (ANOVA model comparison, χ^2 test) and comparisons of the Akaike Information Criterion. All tests were two-tailed and considered significant below an alpha level of 0.05.

We first ran a GLMM with a binomial error distribution and logit-link function to assess whether there was a difference in the number of adult individuals that participated in grooming behaviour; our response measure was a binary term – did the individual engage in any grooming (Yes or No). For those individuals that did participate in grooming, we ran Gaussian LMMs to understand this behaviour further (only including grooming bouts >5 s; Kern and Radford 2018). We first analysed the proportion of time that individuals spent grooming (summed grooming durations for each individual divided by the time available for grooming at the refuge, with the latter defined as the duration between the first and last grooming bout). We then used additional LMMs to consider whether the increase in proportion of time grooming (see *Results*) was driven by a greater frequency (number of grooming interactions each individual was involved in divided by the time available for grooming at the refuge) and/or an increase in mean bout duration; this hierarchical approach avoids the inflation of Type I errors. We subsequently ran Wilcoxon signed-rank tests in SPSS 24 (as in *Observational Data Collection* and *Experiment 1 Protocol*) to consider the grooming behaviour between specific categories of group members (see *Results*).

Chapter 3: Experimental Field Evidence That Outgroup Threats Influence Within-group Behaviour

Morris-Drake A., Christensen, C., Kern J. M., Radford A. N. Experimental field evidence that outgroup threats influence within-group behaviour. Behavioral Ecology 30: 1425–1435.

Chapter Three is presented as the published version with the Supplementary Material from the paper in Appendix 1 at the end of the chapter.

AMD co-designed the study, maintained the habituated study population, conducted the fieldwork, carried out the data analysis, interpreted the results and drafted the manuscript; CC co-designed the study and commented on the manuscript; JMK established and maintained the habituated study population and commented on the manuscript; ANR co-designed the study, advised on data analysis and commented on the manuscript.

3.1 Abstract

In social species, conspecific outsiders present various threats to groups and their members. These outgroup threats are predicted to affect subsequent within-group interactions (e.g. affiliation and aggression) and individual behaviour (e.g. foraging and vigilance decisions). However, experimental investigations of such consequences are rare, especially in natural conditions. We used field-based call playbacks and faecal presentations on habituated wild dwarf mongooses (*Helogale parvula*)—a cooperatively breeding, territorial species—to examine post-interaction responses to the simulated threat of a rival group. Dwarf mongooses invested more in grooming of groupmates, foraged closer together and more regularly acted as sentinels (a raised guard) after encountering indicators of rival-group presence compared to control conditions. These behavioural changes likely arise from greater anxiety and, in the case of increased vigilance, the need to seek additional information about the threat. The influence of an outgroup threat lasted at least 1 h but individuals of different dominance status and sex responded similarly, potentially because all group members suffer costs if a contest with rivals is lost. Our results provide field-based experimental evidence from wild animals that outgroup threats can influence within-group behaviour and decision-making, and suggest the need for greater consideration of the lasting impacts of social conflict.

3.2 Introduction

In many social species, groups and their members face a variety of threats from conspecific outsiders but relatively little is known about the consequences of these so-called outgroup threats. From hymenopterans to humans, individuals form stable permanent groups which often defend collective resources (Radford 2003; Kitchen and Beehner 2007; Batchelor and Briffa 2011; Christensen and Radford 2018). Outgroup threats range from individuals seeking reproductive opportunities (Mares et al. 2011; Bruintjes et al. 2016), to single-sex groups looking to usurp dominant individuals (Ridley 2012), to whole groups attempting to acquire access to limited resources, such as food, mates and sleeping sites (Wilson and Wrangham 2003; Kitchen and Beehner 2007; Golabek et al. 2012). A large literature exists on the immediate defensive behaviours and decisions relating to contests between rivals, considering who participates, the type of interaction (signalling exchanges to physical fighting), and what factors influence the outcome (Radford 2003; Radford and Du Plessis 2004*b*; Majolo et al. 2005; Kitchen and Beehner 2007; Desjardins et al. 2008; Willems et al. 2015). Far less attention has been paid to the wider consequences of outgroup threats, beyond the actual interactions with outsiders or indicators of their presence (e.g. scent-marks), despite their importance for a full understanding of the costs and benefits of social conflict (Radford et al. 2016).

Alterations in within-group behaviour in response to outgroup threats are predicted, but experimental testing of these ideas is rare in nonhuman animals. There are strong theoretical arguments for why within-group affiliative and aggressive interactions are expected to change as a consequence of conflict with outsiders (Hamilton 1975; Reeve and Hölldobler 2007; Radford et al. 2016). From a proximate perspective, behavioural changes may result from conflict-induced increases in anxiety; functionally, affiliation may be used as a reward and to strengthen social bonds, whilst aggression may be a form of punishment (Radford et al. 2016). Correlational data have indicated an influence of outgroup conflict: allopreening between green woodhoopoe (*Phoeniculus purpureus*) groupmates was elevated both immediately after intergroup contests and many hours later (Radford 2008*a*; Radford and Fawcett 2014), whilst vervet monkeys (*Chlorocebus pygerythrus*) exhibited greater levels of both within-group affiliation and aggression during extended bouts of intergroup conflict (Arseneau-Robar et al. 2016, 2018). In captive experiments, cichlid fish (*Neolamprologus pulcher*) increased affiliative interactions with groupmates after simulated intrusions by outgroup rivals (Bruintjes et al. 2016), and tufted capuchin monkeys (*Cebus apella*) increased aggression levels during, but not after, outgroup encounters (Polizzi di Sorrentino et al. 2012). However, we know of only one experimental study testing these ideas in the wild: green woodhoopoes increased their allopreening more following playback of vocal choruses from non-neighbouring groups compared to

those from neighbouring groups (Radford 2008*b*). Moreover, changes in behaviours other than affiliation and aggression are expected in response to outgroup conflict (Radford et al. 2016). Whilst research on individual and pair-bonded territory holders has shown, for instance, increased vigilance and reduced foraging following territorial intrusions (Olendorf et al. 2004; Descovich et al. 2012), experimental tests of such effects have not been conducted in group-living species (Christensen and Radford 2018).

Post-interaction responses to outgroup threats are expected to differ depending on the characteristics of individual group members. The interests and motivations of group members are unlikely to be perfectly aligned because of differences in, for example, sex, age, kinship and dominance status (Heinsohn and Packer 1995; Radford et al. 2016). It is well known that individuals vary in their levels of defensive participation when encountering an outgroup threat (Majolo et al. 2005; Kitchen and Beehner 2007; Schindler and Radford 2018). However, few studies have empirically tested how groupmates differ in their post-interaction behaviour (Radford et al. 2016). There are two examples where the effect of dominance status has been explored: correlational data from wild green woodhoopoes indicated that the post-interaction increase in affiliation is driven by the dominant breeding pair (Radford 2008*a*), whereas the equivalent affiliation increase seen in captive cichlids is driven by subordinates (Bruintjes et al. 2016). Observational data from wild vervet monkeys has been used to consider sex differences in within-group affiliation and aggression during intergroup encounters (Arseneau-Robar et al. 2016, 2018). Field experiments are now needed to investigate further how within-group dynamics are affected by outgroup threats.

The level of perceived outgroup threat is also likely to affect post-interaction behaviour. One well-studied contributor to threat level is rival-group identity: in some species, strangers are a greater threat than neighbours (resulting in a dear-enemy effect); in other cases, neighbours are more of a threat than strangers (the nasty-neighbour effect) (Radford 2005; Müller and Manser 2007; Christensen and Radford 2018). These differences have been shown to influence post-interaction behaviour in green woodhoopoes and cichlid fish (Radford 2008*b*; Bruintjes et al. 2016). Another element of threat level is the intensity of an intergroup interaction, which can range from the exchanging of information (Mirville et al. 2018*a*) through signalling contests (Radford 2003) to physical fights (Mitani et al. 2010). There is some evidence from correlational data that interaction intensity can affect subsequent behaviour (Radford 2008*a*; Radford and Fawcett 2014). A less-considered aspect of threat level is the likelihood of an outgroup contest arising (Radford 2011). Various cues can provide information on the current or recent presence of rivals. For instance, many social species

produce regular within-group vocalisations (Palombit et al. 1999; Radford and Ridley 2008; Townsend et al. 2011) which would reveal the proximity of a rival group; mammals commonly demarcate their territorial boundaries by depositing scent-marks (e.g. urine, faeces, anal-gland secretions) at communal latrines (Brown and Macdonald 1985), indicating rival presence sometime in the past. Animals might, therefore, be expected to behave differently following detection of cues that indicate different likelihoods of an imminent outgroup contest.

In this study, we experimentally investigate within-group behavioural responses to outgroup threats in wild dwarf mongooses (*Helogale parvula*), an ideal model species for biological and logistical reasons. Dwarf mongooses are cooperative breeders, living in family groups comprising a dominant breeding pair and non-breeding subordinates of both sexes (Rasa 1977). Group members sleep, forage and travel together within a shared territory (Rood 1983; Kern and Radford 2013; Christensen et al. 2016). At the sleeping burrow in the morning and evening, within-group affiliation is displayed frequently via the grooming of others (Kern and Radford 2016, 2018). Throughout the day, individuals make constant decisions relating to foraging (e.g. how close to forage near a groupmate; Kern and Radford in revision) and vigilance (e.g. whether and when to act as a sentinel; Kern and Radford 2014, 2017). Each group has one or more conspecific neighbours; territorial behaviour involves scent-marking at communal latrines and physical defence when rivals are encountered (Rasa 1973*c*; Christensen et al. 2016). Latrines are usually visited as a group and scent-marks (urine, faeces, cheek gland and anal gland secretions) are deposited by multiple group members. The ability to habituate wild dwarf mongooses to the close presence of human observers allows the collection of ecologically valid data and the running of experiments in natural conditions (Kern and Radford 2013, 2014, 2016, 2018; Christensen et al. 2016; Morris-Drake et al. 2016, 2017).

We conducted two field-based experimental manipulations to determine individual behavioural responses to outgroup threats. First, we considered how affiliative (grooming) and aggressive within-group interactions are affected by a simulated outgroup threat (playback of close calls to indicate a rival group nearby). Second, we considered whether the threat of a rival group influences individual foraging and vigilance decisions, and how those responses are affected by potential variation in the threat level; we played back rival-group close calls to represent a threat from a nearby group and presented rival-group faeces to represent a lesser threat (as those who deposited the faeces may have moved away). We predicted that, as a consequence of increased anxiety and need for additional information about the threat, individuals would display more within-group grooming and aggression, forage closer together and contribute more to sentinel behaviour after the

simulated presence of a rival group compared to control conditions. We expected dominant individuals to show stronger responses than subordinates as the former are likely to suffer the greatest costs if rival groups gain access to limited resources (e.g. food, mates and sleeping sites). We also expected females to contribute more than males after rival treatments because females are the philopatric sex in dwarf mongooses (Rood 1987); the retention or loss of resources has potentially longer-term consequences for the philopatric sex. Finally, we predicted a stronger response to rival-group call playbacks than faecal presentations as the former could indicate the possibility of a more imminent contest.

3.3 Methods

3.3.1 Study Site and Population

Data were collected from a habituated wild population of dwarf mongooses as part of the long-term Dwarf Mongoose Research Project (DMRP). This work was conducted on Sorabi Rock Lodge, a private game reserve in the Limpopo Province, South Africa (24° 11'S, 30° 46'E); full details available in Kern and Radford (2013). Experimental data were collected over two periods (October 2015 to February 2016 and July–September 2017) on seven wild groups (mean±SD group size: 10.9±5.2, range: 4–17); data were obtained from all habituated groups available at the time. Groups were habituated to close human presence (<5 m), facilitating controlled experimental manipulations in natural conditions. All work was conducted under permission from the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001-CPM403-00013) and the Ethical Review Group, University of Bristol (University Investigator Number: UIN/17/074).

Individuals can be identified from distinctive physical features or from small marks of blonde dye (Garnier Nutrisse) applied to their fur (Kern and Radford 2013). The population has been studied since 2011 and the dominance status and sex of all individuals is therefore known. The dominant pair in a group are recognised through observations of aggressive behaviour, foraging displacements and scent-marking, whilst individuals are sexed through observations of ano-genital grooming (Kern and Radford 2016). Data were only collected from adults (individuals older than 12 months) as juveniles do not routinely engage in at least some of the measured behaviours (e.g. sentinel activity) (Kern et al. 2016).

3.3.2 Field Experiments

Two field-based experiments were conducted to investigate within-group behavioural responses to simulated outgroup threats. In Experiment 1, seven groups each received two treatments at their

morning sleeping burrow: (i) playback of the close calls of a non-neighbouring group (one that did not share any territorial boundaries with the focal group); and (ii) playback of herbivore grunts and huffs (as a control). The immediate responses to the playback and subsequent within-group affiliative (grooming) and aggressive interactions were recorded. In Experiment 2, seven groups each received four treatments whilst foraging: (i) playback of the close calls of a non-neighbouring group; (ii) playback of herbivore grunts and huffs (as a control); (iii) presentation of faeces from the same non-neighbouring group as in (i); and (iv) presentation of herbivore faeces (as a control). The immediate responses to playback and faecal presentations, as well as subsequent foraging and vigilance decisions, were recorded. Non-neighbouring groups are encountered naturally in the wild (Rasa 1987; Sharpe et al. 2015) and were chosen to avoid restrictions associated with using neighbouring group stimuli; namely, only being able to run experimental trials in certain areas of a territory (i.e. the area that overlaps with that particular neighbour).

3.3.2.1 Playback and faecal stimuli

Playback stimuli were constructed from original sound recordings. All sound recordings were made with a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a Sennheiser directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Recordings were made at a sampling rate of 48 kHz with a 24-bit resolution and stored on a Transcend SD card (Transcend, Taipei, Taiwan). Dwarf mongooses are very vocal and rely on acoustic communication to coordinate their cooperative behaviours; they produce close calls (low-amplitude vocalisations) continuously whilst foraging and moving (Sharpe et al. 2013). Close calls therefore provide a vocal cue as to the presence of another group; unlike some other species (Radford 2003; Golabek and Radford 2013), dwarf mongooses do not produce a particular vocalisation during encounters with rival groups that indicates more directly an outgroup threat (personal observation). Close calls were recorded *ad libitum* from four randomly chosen adult individuals in each group, including one or both dominants and either two or three subordinates accordingly. Recordings were made from 1–2 m during behavioural observation sessions in calm weather conditions. The peak sound-pressure level (SPLA) of close calls was measured (in dB) using a HandyMAN TEK 1345 sound meter (Metrel UK Ltd., Normanton, UK) to standardise playback volume at natural levels in experimental trials. Herbivore sounds were recorded in calm weather conditions from the vicinity of the main lodge at the study site, where a variety of ungulate species, including zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis giraffe*), blue wildebeest (*Connochaetes taurinus*) and waterbuck (*Kobus ellipsiprymnus*), are

accustomed to human presence. The microphone was attached to a tree 10 m from an artificial feeding area and left to record for 1 h.

Five-minute playback tracks were constructed in Audacity (version 2.1.3). For rival-group tracks, close calls with good signal-to-noise ratio were randomly chosen and extracted from original recordings. Four different call sequences were constructed per group, with each sequence consisting of one close call from each of the four recorded individuals. These sequences were selected in a random order and inserted into a 12 s block of ambient sound; ambient-sound recordings were made from the centre of the relevant territory with the equipment described above. Five such 12 s blocks were edited together, and this 1 min block was copied five times to create a 5 min track. Rival-group tracks had a close-call rate of 75 calls per minute, which is the natural vocalisation rate of four dwarf mongooses (Sharpe et al. 2013). Control tracks consisted of randomly chosen herbivore sounds (zebra and wildebeest grunts or huffs) with good signal-to-noise ratio that were extracted from original recordings. For each track, four different sequences were generated, each consisting of four unique herbivore sounds. These sequences were randomly selected and inserted into five 12 s blocks of ambient sound, which were then copied to create a 5 min track with 20 herbivore sounds per minute. In all playback tracks, sounds were gradually faded in with increasing amplitude to simulate an approach. At the midway point of each track, the amplitude was 55 dB SPLA at 1 m, which is the natural volume of dwarf mongoose close calls (see above). Different rival-group and control tracks were constructed for trials to different groups.

Faecal collection, storage and usage followed the protocol previously used on this study population by Christensen et al. (2016). Freshly deposited dwarf mongoose faeces were collected immediately and placed in airtight plastic bags inside glass pots whilst in the field. Faeces were refrigerated (5°C) on return to the field base and always used in an experimental presentation the following day. Each presented sample consisted of one deposit from four different adult individuals, including at least one dominant group member. For the control treatment, four fresh waterbuck or giraffe faecal pellets (both similar in diameter to dwarf mongoose faeces) were collected from the vicinity of the main lodge at the study site. Storage and usage protocols matched those for dwarf mongoose faeces. Different rival-group and control faeces were used for each trial.

3.3.2.2 General experimental protocol

For each experiment, trials to a given group were carried out on separate days and completed within 1 week for Experiment 1 (mean±SE: 3.4±0.7 days, range: 1–5 days) and 1 month for Experiment 2

(mean±SE: 11.8±3.3 days, range: 4–30 days). Treatment order was counterbalanced between groups. Trials were not conducted if there had been an intergroup interaction earlier that day and were abandoned if an alarm call or any other group disturbance (e.g. snake mob) occurred during the experimental manipulation (Experiment 1: N=3; Experiment 2: N=5). Abandoned trials were re-run another day when the above conditions were met. Behavioural responses in all trials were recorded to a Dictaphone (ICD-PX312, Sony, Sony Europe Limited, Surrey, UK); collecting data through live observation allowed a wider field of view and consideration of more group members than video recording, but precluded blind scoring. The location of each experimental manipulation was recorded using a GPS (Garmin Etrex H GPS; Garmin Europe Ltd., Southampton, Hampshire, UK). Analysis of the GPS data revealed that there was no significant difference between the different treatments in an experiment in the likelihood that they were run in the core or the periphery of the focal group's territory (Appendix 1: Experimental Location).

Playback trials followed our standard general protocol (Kern and Radford 2014, 2017, 2018). Trials took place when there had been no alarm call or group disturbance for at least 10 min. Tracks were played from an iPod (Apple, Cupertino, California, USA) through a portable SME-AFS field loudspeaker (Saul Mineroff Electronics Inc., New York, USA), which was concealed in vegetation (Experiment 1: near the sleeping burrow; Experiment 2: near the foraging group). The mongooses were attracted to a location 5 m from the loudspeaker using a small amount of hard-boiled egg. Once 50% of the adults in the group were present, the relevant playback track was started and dictation of behaviour commenced. The following immediate responses to the playback were determined for adults within 5 m of the loudspeaker: whether an individual looked and orientated (whole body pointing towards the loudspeaker) in the direction of the loudspeaker; and whether an individual interrupted foraging and directly approached the loudspeaker.

Faecal trials followed the general protocol in Christensen et al. (2016), with presentations conducted at known dwarf mongoose latrines. Once the group left the morning sleeping burrow to start foraging, the presence of nearby latrines (recorded as part of DMRP daily data collection) was tracked using the map page on the GPS. When the group appeared to be approaching a known latrine, the observer moved ahead and placed the relevant faecal samples at the site. The observer then attracted the mongooses to a location 5 m from the latrine using a small amount of hard-boiled egg. Once 50% of the adults in the group were present, dictation of behaviour commenced; a trial was deemed to have started once the first individual approached the latrine. The following immediate responses of adults to the faecal presentation were determined: the number and identity of

individuals that participated in the latrine; and the number and duration of all occasions that individuals sniffed the presentation.

3.3.2.3 Specific protocols for individual experiments

For Experiment 1, both sound treatments to the same group (rival-group playback and control playback) were conducted at the same type of sleeping burrow (always termite mounds) when weather conditions were calm. The playback equipment was set up before the first mongoose emerged; the field loudspeaker was hidden from view 5 m from the burrow. Two minutes after all the group members had emerged, the mongooses were attracted to a location 5 m from the loudspeaker and the trial commenced (see *General experimental protocol*). When the playback track ended, data on within-group behavioural interactions were dictated until 50% of the group had left to start foraging. All aggressive and affiliative (grooming) interactions between adult individuals were recorded, including the identity of those involved and the duration of the interactive bout.

For Experiment 2, all four treatments to the same group (rival-group and control playbacks and presentations of rival-group and control faeces) were conducted when the group was foraging in a similar habitat type during calm weather conditions. Trials were run as per the *General experimental protocol*. Groups were followed for an hour after the experimental manipulations, during which nearest-neighbour scans were conducted every 10 min and sentinel scans were conducted every 5 min. Nearest-neighbour scans entailed estimating the distance (to the nearest 0.5 m) of the closest group member to all foraging individuals in sight; it was not possible to record individual identities regularly without disrupting foragers. Sentinel scans entailed noting whether a sentinel was present and, if so, its identity and whether it was facing in the direction of the experimental manipulation.

3.3.3 Data Analysis

Mixed models were constructed in RStudio 3.2.2 (R Core Team 2012), while all other analyses were run using SPSS 24 (IBM Corp, 2016). All tests were two-tailed and considered significant at $P<0.05$. Parametric tests were used where the residuals fitted the relevant assumptions of normality and homogeneity of variance. Logarithmic and arcsine transformations were conducted to achieve normality of errors in some cases (details below), otherwise non-parametric tests were used.

For simple paired data, we used Wilcoxon signed-rank tests. As sample sizes were small, P-value calculations based on the default asymptotic distribution of the test statistic would be unreliable; we therefore used the Monte Carlo resampling method (based on 10,000 samples) to

generate P-values. In cases where multiple factors needed to be taken into consideration, repeated-measures ANOVAs, linear mixed models (LMMs) or generalised linear mixed models (GLMMs) (package: lme4; Bates et al. 2015) were used. Mixed models contain fixed and random effects, the latter accounting for repeated trials to the same group or individual within a group. When running mixed models, all fixed effects and two-way interactions of interest were included in the maximal model. Models were refined using Akaike Information Criterion comparisons between candidate model structures, combined with stepwise deletion of non-significant effects (Crawley 2007). The minimal model only contained effects that explained significant variation in the data. P-values were estimated using the drop1 command (using the lmerTest package version 3.1–0 for LMMs) and a graphical approach was used to confirm normality and homoscedasticity of residuals.

3.3.3.1 Experiment 1

To determine if rival-group playbacks induced an increased response relative to control playbacks, and thus simulate an outgroup threat as planned, the immediate responses were considered. Sound-treatment differences in the proportion of individuals that looked and orientated towards the loudspeaker and the proportion of individuals that directly approached the loudspeaker were analysed using Wilcoxon signed-ranks tests.

To examine the influence of sound treatment on subsequent within-group affiliative interactions (there were no aggressive interactions observed), grooming bouts of >5 s were analysed in two stages. First, differences in the overall rate (total number of grooming bouts divided by duration at sleeping burrow) and mean duration of grooming bouts (using all data from each trial combined) were considered using Wilcoxon signed-ranks tests. Second, whether the significant difference in grooming bout duration (see Results) was driven by individuals of different dominance status or sex was considered. Two LMMs (one for dominance status and one for sex), with identity link functions, were run on the raw data. These included sound treatment (rival group, control) and either dominance status (dominant, subordinate) or sex (female, male), as well as their interaction with sound treatment, as fixed effects; individual ID was nested within group ID as the random effects.

3.3.3.2 Experiment 2

To determine if rival-group playbacks and faecal presentations induced an increased response relative to control playbacks and faecal presentations, and thus simulate an outgroup threat as planned, the immediate responses were considered. For the playback trials, sound-treatment differences in the proportion of individuals that looked towards the loudspeaker and the proportion of individuals that

directly approached the loudspeaker were analysed using Wilcoxon signed-ranks tests. For the faecal trials, presentation-treatment differences in the proportion of the group that participated in the latrine and the total time spent sniffing the faeces were analysed using Wilcoxon signed-ranks tests.

To examine the influence of experimental treatment on subsequent within-group foraging decisions, log-transformed mean nearest-neighbour distances during the post-manipulation hour were analysed in a 2x2 repeated-measures ANOVA. Intruder identity (rival group, control), manipulation type (playback, faecal presentation) and their interaction were included as predictor variables. To determine if the experimental treatment had a lasting effect, the nearest-neighbour foraging distances from the first and last scans (10 min and 60 min post-manipulation, respectively) were compared using a second 2x2 repeated-measures ANOVA. The first analysis revealed no difference in nearest-neighbour distances depending on manipulation type (see *Results*), so means were calculated from the two rival-group treatments and the two control treatments for the second ANOVA. Intruder identity (rival group, control), scan period (10 min post-manipulation, 60 min post-manipulation) and their interaction were included as predictor variables in this second ANOVA.

To examine the influence of experimental treatment on subsequent within-group sentinel decisions, arcsine-squareroot-transformed proportions of scan samples in which a sentinel was present were analysed in a 2x2 repeated-measures ANOVA. Intruder identity (rival group, control), manipulation type (playback, faecal presentation) and their interaction were included as predictor variables. The likelihood of sentinels facing in the direction of the experimental manipulation was analysed using a Wilcoxon signed-ranks test for just the period after call playbacks; no individuals acted as a sentinel in the period after a control faecal presentation. Whether the significant difference in sentinel occurrence (see *Results*) was driven by individuals of different dominance status or sex was then considered. Two GLMMs (one for dominance status and one for sex), with binomial error distributions and logit-link functions, were run. Since the first analysis of sentinel behaviour revealed no difference depending on manipulation type (see *Results*), values were combined for the two rival-group treatments and the two control treatments. The models bound the number of scan samples in which an individual was on sentinel duty with the number of scan samples in which the individual was not acting as a sentinel, testing the likelihood of an individual being on sentinel duty over a given period. The fixed effects applied to these models were intruder identity (rival group, control) and either dominance status (dominant, subordinate) or sex (female, male), as well as their interaction with intruder identity; individual ID was nested within group ID as the random effects.

3.4 Results

3.4.1 Experiment 1

The immediate responses to playback at the sleeping burrow were significantly affected by sound treatment. A greater proportion of individuals looked and orientated towards the loudspeaker during rival-group playback compared to control playback (Wilcoxon signed-ranks test: Z=2.379, N=7, P=0.014; Figure 3.1a). A greater proportion of individuals also approached the loudspeaker directly during playback of a rival group compared to control playback (Z=2.201, N=7, P=0.030; Figure 3.1b).

Subsequent within-group responses to playback were significantly affected by sound treatment. No aggressive interactions were observed following either sound treatment, but affiliative (grooming) interactions were common (mean±SD grooming rate: 0.5±0.3 bouts per minute). Although there was no significant sound-treatment difference in the overall rate of grooming interactions (Wilcoxon signed-ranks test: Z=0.676, N=7, P=0.576; Figure 3.1c), grooming bouts were longer after playback of a rival group compared to a control playback (Z=2.366, N=7, P=0.015; Figure 3.1d). Grooming-bout duration was not significantly affected by the interaction between treatment type (control, rival) and either dominance status (LMM: χ^2=0.348, df=1, P=0.560; Table 3.1a) or sex (χ^2=0.001, df=1, P=0.973; Table 3.1b); dominant and subordinate individuals responded similarly to the outgroup threat, as did males and females.

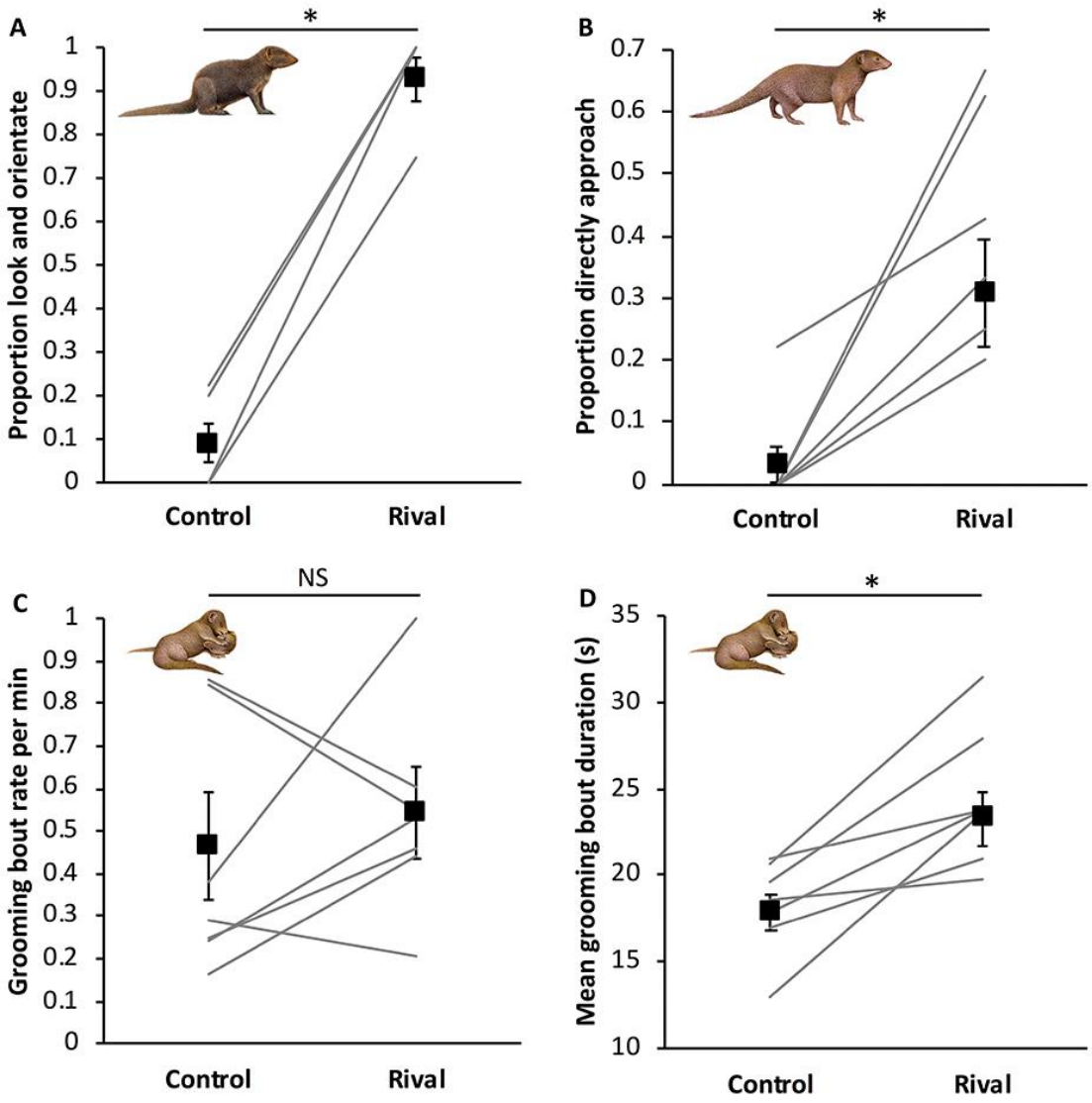

Figure 3.1 Immediate (a,b) and subsequent (c,d) responses of dwarf mongooses to control (herbivore) and rival-group playbacks (N=7 groups). Shown in all panels are the values for each group (connected by solid lines; the data values for some groups are the same, thus the number of lines can appear less than 7) and the overall treatment mean (solid squares) ± SE. NS=non-significant. *=P<0.05.

Table 3.1 Output from LMMs (a,b) and GLMMs (c,d) investigating whether the significant difference in grooming-bout duration was driven by individuals of different dominance status or sex (a,b) and whether the significant difference in sentinel occurrence was driven by individuals of different dominance status or sex (c,d). Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Mean grooming-bout duration by dominance status					
Random effects	*Group ID*	1.153			
	Individual ID in Group ID	2.472			
Minimal model	(Intercept)	18.423±1.520			
	Trial	**7.164±1.949**	**1**	**13.514**	**<0.001**
Removed effects	Trial:Status		1	0.348	0.560
	Status		1	0.022	0.884
(b) Mean grooming-bout duration by sex					
Random effects	*Group ID*	1.153			
	Individual ID in Group ID	2.472			
Minimal model	(Intercept)	18.423±1.520			
	Trial	**7.164±1.949**	**1**	**13.514**	**<0.001**
Removed effects	Trial:Sex		1	0.001	0.973
	Sex		1	0.134	0.718
(c) Proportion of scan samples with a sentinel present by dominance status					
Random effects	*Group ID*	0.649			
	Individual ID in Group ID	0.043			
Minimal model	(Intercept)	3.111±0.284			
	Trial	**1.837±0.211**	**1**	**100.462**	**<0.001**
	Status	**0.956±0.287**	**1**	**9.717**	**0.002**
Removed effects	Trial:Status		1	0.901	0.343
(d) Proportion of scan samples with a sentinel present by sex					
Random effects	*Group ID*	0.797			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	3.769±0.002			
	Trial	**1.836±0.002**	**1**	**100.400**	**<0.001**
Removed effects	Trial:Sex		1	1.815	0.178
	Sex		1	0.956	0.328

3.4.2 Experiment 2

The immediate responses to experimental trials were significantly affected by intruder identity. As in Experiment 1, a greater proportion of individuals looked at the loudspeaker (Wilcoxon signed-ranks test: Z=2.366, N=7, P=0.015; Figure 3.2a) and directly approached the loudspeaker (Z=2.366, N=7, P=0.015; Figure 3.2b) during rival-group playback compared to control playback. As in Christensen et al. (2016), there was a significantly greater proportion of individuals participating in the latrine event (Z=2.201, N=7, P=0.035; Figure 3.2c) and a significantly longer total time spent sniffing the faeces (Z=2.366, N=7, P=0.015; Figure 3.2d) in response to rival-group faeces compared to control faeces.

Foraging decisions in the hour after the manipulation were affected by intruder identity (rival, control), but not manipulation type (playback, faecal presentation). Overall, individuals foraged significantly closer to another group member following rival-group playbacks and faecal presentations compared to control treatments (repeated-measures ANOVA: $F_{1,6}$=8.995, P=0.024; Figure 3.3a,b), irrespective of manipulation type (main effect: $F_{1,6}$=0.017, P=0.900; interaction with intruder identity: $F_{1,6}$=0.107, P=0.755). The stronger response to rival-group treatments compared to control treatments lasted for at least 1 h after the simulated intrusion: there was no significant effect of scan period (10 min, 60 min post-manipulation) on nearest-neighbour distances ($F_{1,6}$=0.046, P=0.838; interaction with intruder identity: $F_{1,6}$=0.677, P=0.442).

Sentinel decisions in the hour after the manipulation were similarly affected by intruder identity. Overall, there was significantly more sentinel behaviour following rival-group playbacks and faecal presentations compared to control treatments (repeated-measures ANOVA: $F_{1,6}$=30.274, P=0.002; Figure 3.3c,d), irrespective of manipulation type (main effect: $F_{1,6}$=0.542, P=0.489; interaction with intruder identity: $F_{1,6}$=0.270, P=0.622). Moreover, a greater proportion of sentinels were facing in the direction of the manipulation after rival-group playback compared to control playback (Wilcoxon signed-ranks test: Z=2.366, N=7, P=0.015). There was no significant effect of the interaction between treatment type (control, rival) and either dominance status (GLMM: χ^2=0.901, df=1, P=0.343; Table 3.1c) or sex (χ^2=1.815, df=1, P=0.178; Table 3.1d) on post-manipulation sentinel behaviour; dominant and subordinate individuals responded similarly to the outgroup threat, as did males and females.

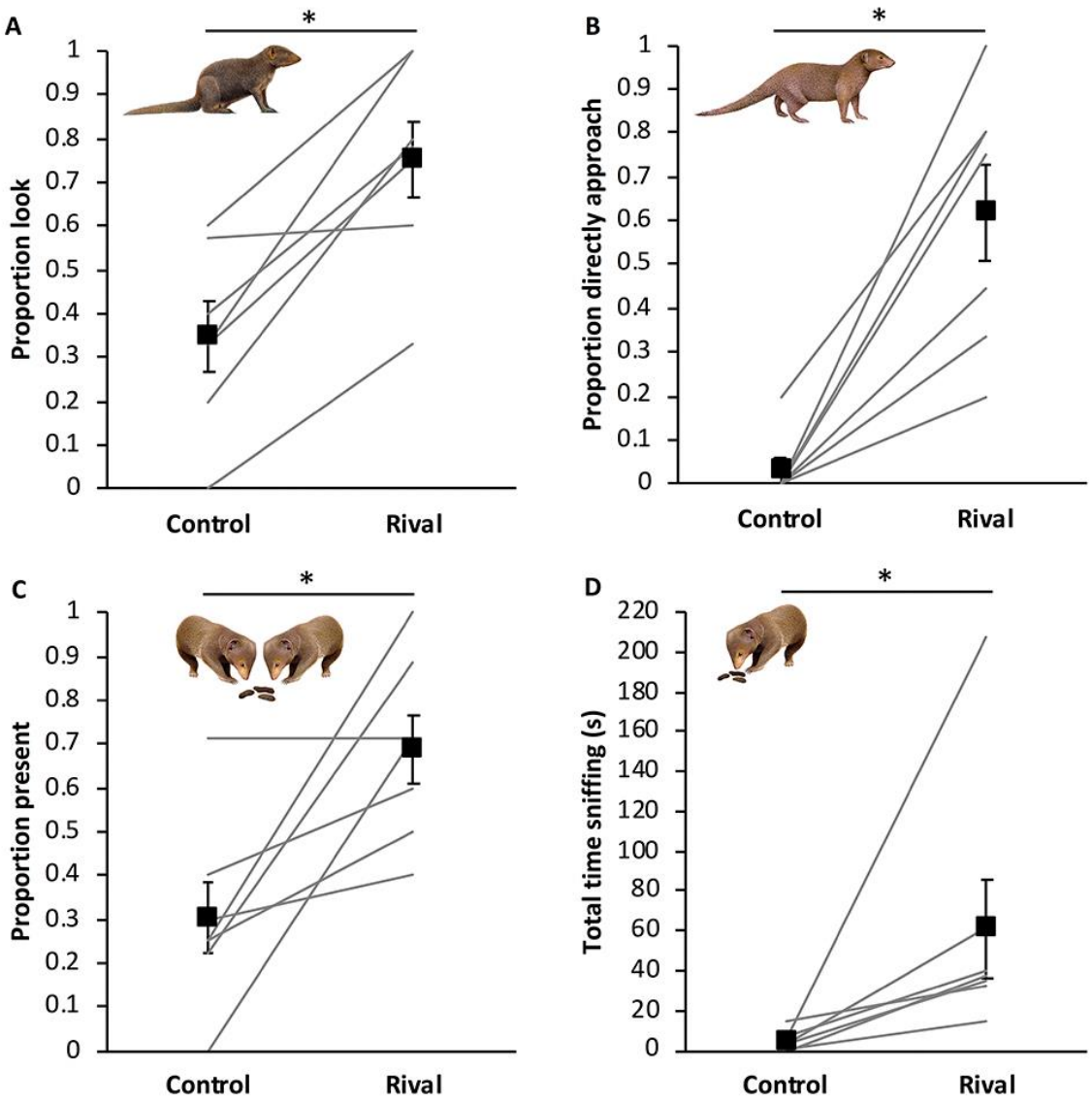

Figure 3.2 Immediate responses of dwarf mongooses to control (herbivore) and rival-group (a,b) playbacks and (c,d) faecal presentations (N=7 groups). Shown in all panels are the values for each group (connected by solid lines) and the overall treatment mean (solid squares) ± SE. *=P<0.05.

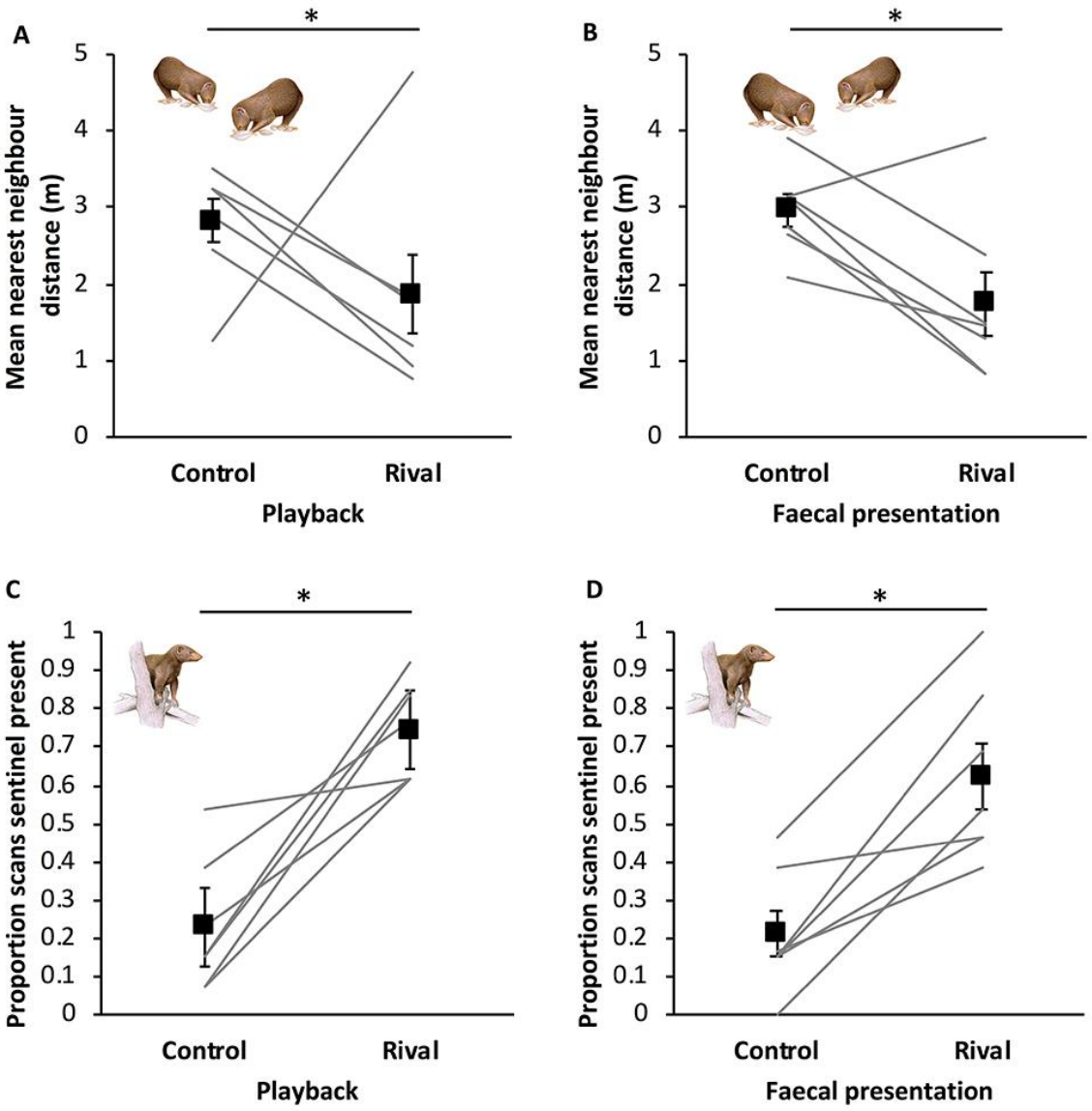

Figure 3.3 Foraging (a, b) and sentinel (c, d) responses of dwarf mongooses to control (herbivore) and rival-group playbacks and faecal presentations (N=7 groups). Shown in all panels are the values for each group (connected by solid lines) and the overall treatment mean (solid squares) ± SE. *=P<0.05.

3.5 Discussion

Following a simulated threat from a rival group, dwarf mongooses invested more in grooming, foraged closer together and conducted more sentinel behaviour than in control trials. Previous observational studies of birds and primates (Radford 2008*a*; Arseneau-Robar et al. 2016), and an experimental study with captive fish (Bruintjes et al. 2016), have also found an increase in affiliation among groupmates as a consequence of outgroup conflict; alterations in foraging and vigilance have not previously been examined in an outgroup context. In principle, the behavioural changes following rival-group playbacks and faecal presentations cf. control treatments could simply be a response to any mongoose stimulus. However, Christensen et al. (2016) showed a stronger response to rival-group faeces than own-group faeces, with no difference in response to herbivore and own-group faeces, and we found a similar pattern of responses to rival-group, own-group and herbivore playbacks (Appendix 1: Extra Experiment). We are therefore confident that our results represent a response to rival-group stimuli rather than mongoose stimuli *per se*, and that our study provides rare experimental evidence from a wild population that outgroup threats influence within-group behaviour (see also Radford 2008*b*).

Increased anxiety arising from outgroup conflict is likely to play a role in driving changes to within-group interactions. Conflict induces anxiety, not least because of the risks of potential injury or death, disrupted relationships or lost resources (Aureli et al. 2002; Radford et al. 2016). A proximate reason for increased post-interaction affiliation (such as the elevated grooming observed in the mongooses) is anxiety reduction, since both the giving and receiving of grooming is known to have this benefit in mammals and birds (von Holst 1998; Aureli et al. 1999; Aureli and Yates 2010; Radford 2012). Functionally, increased affiliation could act as a reward for recent participation and/or as an incentive for future help in interactions with outgroup rivals (Radford 2008a, 2011; Arseneau-Robar et al. 2016; Radford et al. 2016). Whilst greater anxiety might potentially also lead to increased within-group aggression, either as a byproduct or if it is used to punish free-riders (Radford et al. 2016; Arseneau-Robar et al. 2016, 2018), no aggression was seen between dwarf mongoose groupmates following rival-group playbacks at the sleeping burrow. As within-group aggression is generally more prevalent in this species when group members are foraging (personal observation), perhaps an effect of outgroup conflict on antagonistic interactions might be observed at these times.

Foraging closer to others in the aftermath of a simulated outgroup threat may also be a consequence of increased anxiety. As is the case following within-group conflict (Verbeek and de Waal 1997; Mallavarapu et al. 2006), close proximity to other group members could function directly to reduce anxiety. Moreover, as in response to increased predation risk (e.g. Bell et al. 2009), groupmates

may forage closer together when there is a higher likelihood of a contest with outsiders if that means enhanced support or some dilution of the personal risk. These benefits might be particularly apparent if individuals forage near close affiliates (Young et al. 2014); the existence of close affiliations can generally lower anxiety levels through social buffering (Cohen and Wills 1985; Wittig et al. 2008). Dwarf mongooses exhibit social bonds of different strengths with different groupmates (Kern and Radford 2016), but future work would be needed to examine such detailed foraging relationships following stressful events.

Increased vigilance following cues of rival group presence could result from greater anxiety or a need to gather more information about the threat. Sentinels are suggested to be in a safer position than foragers, at least from a predatory threat (Bednekoff 1997; Wright et al. 2001). Whether the same applies in an outgroup context is unknown, but if this was driving the changes seen then several individuals might be expected to adopt a raised position at the same time and that was rarely the case in our study. More likely, perhaps, is that the increase in sentinel activity reflects an attempt to obtain additional information. Traditionally, sentinel behaviour is discussed in an antipredator context (Bednekoff 2015). However, individuals may also act as sentinels for other reasons, such as to gain information about dispersal or mating opportunities (Walker et al. 2016). In the current context, they may do so because there has been an indication of a rival group (from secondary cues such as vocalisations or faeces) but no visual sign of those outsiders. Our experimental manipulations represent a likely common occurrence as dwarf mongooses regularly encounter faeces of other groups at latrines (Christensen et al. 2016) and the thick vegetation may mean that lines of sight are obscured and the producers of vocalisations cannot easily be detected visually, especially by foragers on the ground. Information on the location of the group that is calling or has deposited faeces, as well as other knowledge such as their group size, is likely valuable in terms of subsequent decision-making.

The few previous empirical studies on the consequences of outgroup conflict have tended to focus on just whether there is an effect in the immediate aftermath of an interaction. As an exception, Radford and Fawcett (2014) provided correlational evidence that outgroup contests affect decision-making and group cohesion over the course of a day. Green woodhoopoe groups that had an intense intergroup interaction in the morning were more likely to roost in the zone of conflict that evening, in addition to being more likely to roost together and to preen one another. Here, we show experimentally that individuals are still foraging closer together (a response to encountering cues of rival-group presence) at least an hour after the manipulation. Investigations of longer-term responses, beyond the immediate effect of elevated anxiety, are crucial if we are to understand fully the range

of costs and benefits at play and will help to shed light on the relationship between intergroup conflict and its suggested role in the evolution of cooperation.

All adults invested in more grooming and sentinel behaviour after exposure to an outgroup threat, regardless of their dominance status and sex. This contrasts previous observational and captive work on woodhoopoes and cichlid fish, which found differences in affiliation between individuals of different dominance status (Radford 2008*a*; Bruintjes et al. 2016). There are at least two possible explanations for a lack of such a finding in our mongoose work. In the cichlid study, there were actual intruders which elicited aggressive defensive actions; in the woodhoopoe study, the playback was of a chorus vocalisation used in adversarial encounters. By contrast, our experiments provided cues to current or recent rival presence; they may not have elicited a full defensive response. Perhaps some dominance or sex variation would be seen in dwarf mongooses if the outgroup interactions escalated. A second potential explanation relates to the perceived threat. The intrusion of a rival group could prove costly for all groupmates if the former are seeking to annex shared resources, such as food, sleeping sites or part of the territory (Wilson and Wrangham 2003; Mitani et al. 2010; Radford and Fawcett 2014). In this case, perhaps all group members would be expected to increase their grooming and sentinel behaviour as our results indicate.

We found no discernible difference in the aftermath responses (sentinel activity, nearest-neighbour foraging distances) to rival playbacks and faecal presentations, contrary to our prediction that the former might indicate a more imminent threat and so elicit a stronger reaction. One possible explanation is that a playback does not fully replicate the circumstances relating to an approaching rival group. Whilst rival playbacks did simulate an outgroup threat, as there were relevant changes in behaviour both during and after the manipulation, our playbacks were not followed by visual confirmation of a rival group. Without such visual validation shortly after hearing acoustic cues indicating a rival group presence, dwarf mongooses might not perceive the situation realistic of an imminent contest. Another potential reason for the lack of a difference between experimental treatment types is that encountering relatively fresh rival faeces at a latrine might have generated similar anxiety to hearing another group. Whilst acoustic cues might suggest an imminent encounter, uncertainty about the current location of the rival group that deposited the faeces might cause equivalent anxiety and thus changes in vigilance and foraging decisions.

Conflict is recognised as a powerful selective force, yet relatively few studies have experimentally investigated the consequences of outgroup conflict despite its prevalence in the

animal kingdom. Both our field manipulations had the predicted effect of simulating an outgroup threat—they resulted in clear changes in immediate and subsequent behaviour—and therefore represent viable approaches for future work. Combining the ecological validity of studying animals in natural conditions with the power from controlled experimental testing allows the generation of strong conclusions about the effects of outgroup threats on within-group behaviours. Together, the two field manipulations provide an insight into three neglected avenues of research in this field: studying a broader range of post-interaction behaviours (beyond aggression and affiliation), looking at behavioural changes from an individual level and focusing on behavioural changes beyond the immediate aftermath (Radford et al. 2016). Future studies should adopt and expand on this approach, across a multitude of species and timeframes, to help unravel how outgroup conflict shapes the lives of social species.

3.6 Appendix 1

3.6.1 Experimental Location

The level of threat from rival groups could vary depending on territorial location (Furrer et al. 2011; Brown 2013). To determine whether the location of experimental trials should to be taken into consideration when analysing the data, we first classified trials as either occurring in the core or periphery of each group's territory. We calculated home ranges using the movement data collected from each group over a 5-month period prior to the experimental field season. The geographical waypoint data from the daily movement maps was transported into MapSource (software version 6.16.3) and then into QGIS (software version 2.14.4) for each group. The minimum convex polygon (MCP) algorithm from the plugin AniMove was used to estimate the full home range (using 100% of the data point fixes; as in Mattisson et al. 2013) and the central 'core' of the home range (using the central 50% of data point fixes). The GPS points of experimental trials were added to each group's territory to determine whether they fell within core (within MCP 50) or peripheral (outside MCP 50) regions as in Jędrzejewski et al. 2007).

To determine whether there was any unintentional bias towards running the experimental manipulations in the core or periphery of each group's territory, Cochran Q and McNemar's tests were carried out. Tests were conducted in RStudio 3.2.2 (R Core Team 2012), were two-tailed and considered significant at $P<0.05$. First, a Cochran Q test was run for the three treatments in the Extra Experiment (see below); whether the trial was conducted in the core (Yes/No) was analysed. Second, two McNemar's tests were run for Experiment 2 (see main chapter text) using the same response variable as above but split for those trials that involved playbacks and those that involved faecal presentations. We were unable to analyse the location data for Experiment 1 as only two out of seven groups differed in their sleeping burrow location between the two trials.

For both the Extra Experiment (see below) and Experiment 2, there was no unintentional bias towards running the experimental trials in the core or periphery of each group's territory (Extra Experiment: Cochran Q test: $Q=2.8$, $df=2$, $P=0.2466$; Experiment 2: McNemar test on playback trials: $\chi^2=0.8$, $df=1$, $P=0.371$; McNemar test on faecal presentation trials: $\chi^2=0.25$, $df=1$, $P=0.617$).

3.6.2 Extra Experiment

To determine whether there was a difference in response to playback of rival-group close calls and own-group close calls, each mongoose group (N=7) was exposed to the following three trials: playback of (i) herbivore (control) sounds, (ii) own-group close calls, and (iii) rival-group close calls. Recordings

and playback track creation followed the same procedure outlined in the main text. Own-group tracks always consisted of calls no more than one month old.

The three trials to a given group were carried out on separate days, always in the morning, when the entire group was foraging in the same habitat type under calm conditions. Each trial was filmed with a HD Panasonic DMC-XS3EB-R video camera (Panasonic House, Berkshire, UK) and a GPS point was taken to mark the experimental location of each trial. Trial order was counterbalanced between groups and all three trials to a given focal group were completed within a two-week timeframe (mean±SE: 4.4±0.8 days, range: 3–9 days). Playbacks took place when there had been no natural alarm call or group disturbance (e.g. snake mob) for at least 10 min. Tracks were played from an Apple iPod (Apple, Cupertino, California, USA) through a portable SME-AFS field speaker (Saul Mineroff Electronics Inc., New York, USA), which was concealed in vegetation along their predicted foraging route. The mongooses were called to a location 5 m away from the loudspeaker using a small amount of hard-boiled egg and once 50% of the adults in the group were present the relevant playback track began. The following immediate responses were extracted from the video recordings of the trials: the number and identity of all the adult group members present at the start of the track; whether an individual looked and orientated (whole body pointing towards the loudspeaker) in the direction of the loudspeaker; and whether an individual directly approached the loudspeaker. Trials were not conducted if an intergroup interaction occurred the morning of the trial and were abandoned if an alarm call, or any other group disturbance, occurred during the playback period (N=1).

To investigate whether there were sound-treatment differences in the proportion of individuals that looked and orientated towards the loudspeaker and the proportion of individuals that directly approached the loudspeaker, Friedman and Wilcoxen signed-ranks tests were carried out. Nonparametric tests were used as the raw and transformed data did not conform with the assumptions of normality and homogeneity of variance. Tests were run using SPSS 24 (IBM Corp, 2016), were two-tailed and considered significant at $P<0.05$. The Monte Carlo method (based on 10,000 samples) was used to calculate significance due to unreliable P-value calculations when sample sizes are small.

The immediate responses to playback were significantly affected by sound treatment. Trial type had a significant effect on the proportion of individuals that looked and orientated towards the loudspeaker (Friedman test: $\chi^2=7.75$, df=2, $P=0.021$), and the proportion of individuals that directly approached the loudspeaker ($\chi^2=8.24$, df=2, $P=0.016$). For both response variables, there was no

significant difference between the two non-threat trials (control and own-group playback): proportion looked and orientated (Wilcoxon matched-pairs signed ranks test: Z=1.473, N=7, P=0.248); and proportion that directly approached (Z=1.089, N=7, P=0.371). However, there was a significantly stronger response to rival-group playback compared to the two non-threat trials (control and own-group playback): a greater proportion looked and orientated during rival-group playback compared to own-group (Z=2.201, N=7, P=0.031) and control playback (Z=2.201, N=7, P=0.030); and a greater proportion directly approached during rival-group playback compared to own-group (Z=2.032, N=7, P=0.045) and control playback (Z=2.207, N=7, P=0.031).

Chapter 4: Experimental Field Evidence For Carryover and Cumulative Effects of Intergroup Conflict

Morris-Drake A., Linden, J. F., Kern J. M., Radford A. N. Experimental field evidence for carryover and cumulative effects of intergroup conflict. In preparation for submission to *Nature Ecology & Evolution*.

Chapter Four is presented as for publication with the Methods appearing at the end of the chapter.

AMD co-designed the study, maintained the habituated study population, conducted the fieldwork, carried out the data analysis, interpreted the results and drafted the manuscript; JFL helped with fieldwork; JMK established and maintained the habituated study population and helped to interpret the results; ANR co-designed the study, advised on data analysis, helped to interpret the results and commented on the manuscript.

4.1 Abstract

Outgroup conflict (the conflict arising between groups and conspecific outsiders) is rife in the natural world. A recent body of work has demonstrated that interactions with rivals or cues of their presence can generate behavioural changes, including to individual vigilance and foraging decisions, within-group affiliation and group movement patterns. However, these studies have focused primarily on the immediate aftermath of outgroup interactions; the minutes or hours following an encounter with rival individuals or groups. Here, we use week-long field-based manipulations with wild dwarf mongooses (*Helogale parvula*) to investigate the potential for longer-term impacts of intergroup conflict. A single presentation of faeces from a rival mongoose group, compared to control herbivore faeces, resulted in a greater level of within-group grooming the following day, providing evidence of a carryover effect beyond the likely period of elevated stress. Repeated presentations of outsider cues led to cumulative effects by the end of the week: compared to control weeks, mongooses exhibited reduced foraging activity and more pronounced inter-individual differences in elevated grooming behaviour, foragers were in closer proximity to one another and individuals were putting on less body mass. Across the week, simulated intrusions of rivals compared to control presentations also resulted in groups spending more time marking their territories and a tendency to fission more often. Our experimental findings provide evidence for longer-term behavioural changes – for carryover and cumulative effects – in response to elevated intergroup threat, which may form the basis for fitness consequences.

4.2 Introduction

In many social species, from ants to humans, groups are in conflict with conspecific outsiders over access to limited resources (Radford 2003; Kitchen and Beehner 2007; Thompson et al. 2017). Single intruders or same-sex groups may attempt to monopolise reproductive opportunities or usurp dominant individuals, whilst whole groups may invade territories and aim to acquire space, food and sleeping sites (Wilson and Wrangham 2003; Mares et al. 2012; Ridley 2012; Bruintjes et al. 2016). An extensive literature exists on how animals behave during outgroup interactions, considering the type of encounter, who contributes during contests and the factors that influence the outcome (Radford 2003; Radford and Du Plessis 2004*b*; Majolo et al. 2005; Kitchen and Beehner 2007; Crofoot et al. 2008; Desjardins et al. 2008; Furrer et al. 2011; Willems et al. 2015; Mirville et al. 2018*b*; Schindler and Radford 2018). Recently, there has been increasing research interest in the behavioural consequences of outgroup conflict (Radford et al. 2016). For instance, there is strong empirical evidence for alterations in within-group affiliation in response to outgroup conflict in a wide range of taxa, such as mammals (Cords 2002; Payne et al. 2003; Arseneau-Robar et al. 2016; Majolo et al. 2016; Morris-Drake et al. 2019; Mirville et al. 2020), birds (Radford 2008*a*, 2008*b*), fish (Bruintjes et al. 2016; Braga Goncalves and Radford 2019) and insects (Birch et al. 2019). Exposure to outgroup threats has also been shown to influence other behaviours, such as group movement patterns and individual decisions about foraging and vigilance (Crofoot 2013; Christensen et al. 2016; Seiler et al. 2018; Morris-Drake et al. 2019). However, the majority of this work has focused on short-term effects (over minutes or hours) both during (Arseneau-Robar et al. 2016; Braga Goncalves and Radford 2019) and in the immediate aftermath (Cords 2002; Payne et al. 2003; Radford 2008*a*, 2008*b*; Bruintjes et al. 2016; Christensen et al. 2016; Morris-Drake et al. 2019; Mirville et al. 2020) of single interactions with outsiders or cues of their presence (but see, Markham et al. 2012; Thompson et al. 2020). To understand fully the effects of outgroup conflict, investigation is also needed of longer-term (carryover) effects from single interactions, cumulative effects from repeated interactions, and how group members differ in their responses.

Single outgroup interactions could potentially have behavioural consequences beyond an immediate period of spatial exclusion or heightened stress. Some short-term behavioural responses to outgroup conflict (e.g. changes in movement patterns) likely arise as a result of temporary territorial exclusion and/or avoidance of conflict zones, and the subsequent reduced access to resources such as preferred foraging locations (Crofoot 2013; Christensen et al. 2016; Mirville et al. 2020). But there are indications from a few observational studies that resource-use decisions could continue to be affected even when spatial access is not restricted (Radford and Fawcett 2014; Dyble et al. 2019). For

instance, green woodhoopoe (*Phoeniculus purpureus*) groups that had engaged in an extended intergroup contest in the morning were more likely than on control days to roost in that area in the evening, even if they had lost the contest (Radford and Fawcett 2014). Since interactions with conspecific outsiders can activate the hypothalamic–pituitary–adrenocortical (HPA) axis, leading to an increase in glucocorticoid (GC) hormone secretion, some additional behavioural changes in the immediate aftermath of outgroup conflicts are likely explained by an acute stress response (Bergman et al. 2005; Engh et al. 2006; Schoof and Jack 2013; Eckardt et al. 2016; Wittig et al. 2016; Samuni et al. 2019). For example, increased within-group affiliation could result because grooming causes a reduction in anxiety (Aureli and van Schaik 1991; Aureli 1997; Aureli et al. 1999; Fraser et al. 2008; Aureli and Yates 2010; Burkett et al. 2016; Wittig et al. 2016). However, grooming may also fulfil a social function—for instance, as a reward for defensive efforts in previous contests or to promote participation in future encounters (Radford 2008*a*, 2008*b*, 2011; Majolo et al. 2016)—and thus increased within-group affiliation might persist even when contest-related elevations in stress levels have dissipated (Radford and Fawcett 2014). This might be especially true if, for example, there is an increased likelihood of another contest occurring in the near future. Experiments are now needed to test the lasting behavioural consequences of outgroup conflict; to consider carryover effects from a single interaction once periods of spatial exclusion and elevated stress have ceased.

Whilst it is logistically simplest for researchers to investigate responses to a single outgroup interaction, prior events and the cumulative build-up of threat are also likely to influence behavioural decisions. As with other stressors (Bejder et al. 2009), previous outgroup interactions might increase (e.g. through sensitisation) or lessen (e.g. through habituation) the responses to a current conflict situation. A recent laboratory-based study on harvester ants (*Messor barbarus*), for example, found evidence for a 'priming' effect: the presentation of a second intruder 20 minutes after the first resulted in an increase in ant activity and contact between groupmates (Birch et al. 2019). Multiple outgroup interactions could also have a cumulative effect (which could be additive or multiplicative); such a build-up of threat could result in behavioural changes not only in the immediate aftermath of each interaction, but also more generally (Thompson et al. 2020). From a proximate perspective, repeated exposure to a stressor could lead to dysregulation of the HPA axis, and consequent changes to baseline behaviour (Sapolsky et al. 2000; Romero 2004). From an ultimate perspective, cumulative effects of outgroup conflict could lead to group members being more affiliative or cooperative, with increases in within-group grooming or a reduced likelihood of group fissions, for example (Radford and Fawcett 2014; Samuni et al. 2017, 2020). Similarly, a greater general threat level might result in higher investment in vigilance or defensive actions (Morris-Drake et al. 2019). Two observational field studies

have suggested a positive link between outgroup interaction frequency and within-group behaviour: green woodhoopoe and chimpanzee (*Pan troglodytes*) groups experiencing more intergroup conflict had higher rates of within-group affiliation and association (Radford 2008*a*; Samuni et al. 2020). However, these results could arise because there are more post-conflict periods, rather than a more general change in baseline behaviour. To investigate fully the cumulative effects of outgroup conflict, we therefore need field experiments to examine behavioural changes outside of the immediate post-conflict period.

Inter-individual differences in responses to outgroup conflict are expected due to variation in benefits and costs. Groups are a heterogenous mix of individuals who differ in, for example, age, sex and dominance status, and it is well-understood that these attributes influence the incentive to engage in outgroup contests as the perceived threat and cost of participation is not the same for all group members (Fashing 2001; Majolo et al. 2005; Kitchen and Beehner 2007; Desjardins et al. 2008). Recent studies have demonstrated that individuals can also differ in within-group behavioural responses to outgroup conflict depending on their sex and dominance status. For example, captive experiments with cichlid fish (*Neolamprologus pulcher*) found that the intrusion of an outsider altered the levels of affiliation and aggression shown towards groupmates but that these varied depending on the donor's own characteristics, as well as those of potential recipients and the identity of the intruder (Bruintjes et al. 2016; Braga Goncalves and Radford 2019). In a field experiment, post-contest increases in within-group affiliation by green woodhoopoes were the result of dominants grooming subordinates more (Radford 2008*b*); an equivalent experimentally induced increase in dwarf mongoose (*Helogale parvula*) grooming was not the consequence of greater affiliation by group members of any particular sex or dominance status (Morris-Drake et al. 2019). To-date, such studies have focused on within-group behaviour during or immediately after a single outgroup interaction; inter-individual differences resulting from the cumulative effect of multiple outgroup events have not been investigated.

Here, we conducted an intergroup-conflict experiment with wild dwarf mongooses to investigate carryover effects from a single simulated territorial intrusion, cumulative effects after repeated simulated intrusions and inter-individual variation in responses. Dwarf mongooses are an ideal species for such a study because they can be habituated to the close presence of observers, allowing experimental manipulations and detailed monitoring in natural conditions (Kern and Radford 2013, 2018; Morris-Drake et al. 2016, 2017). They live in relatively stable, cooperatively breeding groups of up to 30 individuals, comprising a dominant breeding pair and nonbreeding subordinates of

both sexes (Rasa 1977; Kern and Radford 2013). Group members cooperate to defend a shared territory from conspecific rivals (Rood 1983; Christensen et al. 2016). Outgroup interactions range from signal exchanges (mainly visual and/or acoustic) to violent confrontations that can lead to serious injury (personal observation). Recent work has revealed an array of short-term behavioural changes, including increased grooming and sentinel behaviour, and reduced nearest-neighbour foraging distances and group movement, in the hour after a simulated intergroup threat (Christensen et al. 2016; Morris-Drake et al. 2019). In the current study, we simulated multiple territorial intrusions by a rival group across several days and compared behaviours with control periods. In general, we expected this intergroup conflict to result in some changes in individual behaviour the day after a single simulated intrusion, but for there to be greater effects following the cumulative build-up of intergroup threat during the week. Moreover, we expected the cumulative threat of rival groups to have a stronger effect on dominants compared to subordinates, because the former have the most to lose (breeding position, territory) if a rival group invaded (Radford 2008*b*), and on females compared to males, because the former are the philopatric sex in dwarf mongooses (Rood 1987, 1990) and thus the retention or loss of contested resources could have longer-term consequences for females (Cheney and Seyfarth 1987).

4.3 Results

Our field-based repeated-measures experiment entailed two week-long treatments to each of seven dwarf mongoose groups in a counterbalanced order (Figure 4.1). During Days 1–5 of an Intrusion week, we presented the focal group with the simulated presence (faecal samples or call playback) of the same non-neighbouring rival group, replicating a natural situation where rivals encroach into the territory of another group. During a Control week, we presented the focal group with herbivore faeces and call playback on an equivalent schedule to the Intrusion week; herbivore stimuli have been used as controls in previous dwarf mongoose experimental studies examining the short-term consequences of single intergroup intrusions (Christensen et al. 2016; Morris-Drake et al. 2019). We conducted faecal presentations most evenings during treatment weeks (mean±SE: 4.4±0.2, range: 3–5), always at the sleeping burrow, whilst a playback was undertaken mid-week (Day 3 or 4) when the group was out foraging. We used data collected whilst the group was foraging away from the sleeping burrow on Day 2 (the day after the first simulated intrusion) to determine whether there were any carryover effects of single intergroup events on individual behaviours (grooming, foraging, sentinel activity) and body mass. We collected the same data on Day 6 (after repeated simulated intrusions) to investigate possible cumulative effects of intergroup threat. To examine overall

treatment differences in relatively rare group-level behaviours, we also collected data on latrining behaviour and group splits throughout the week.

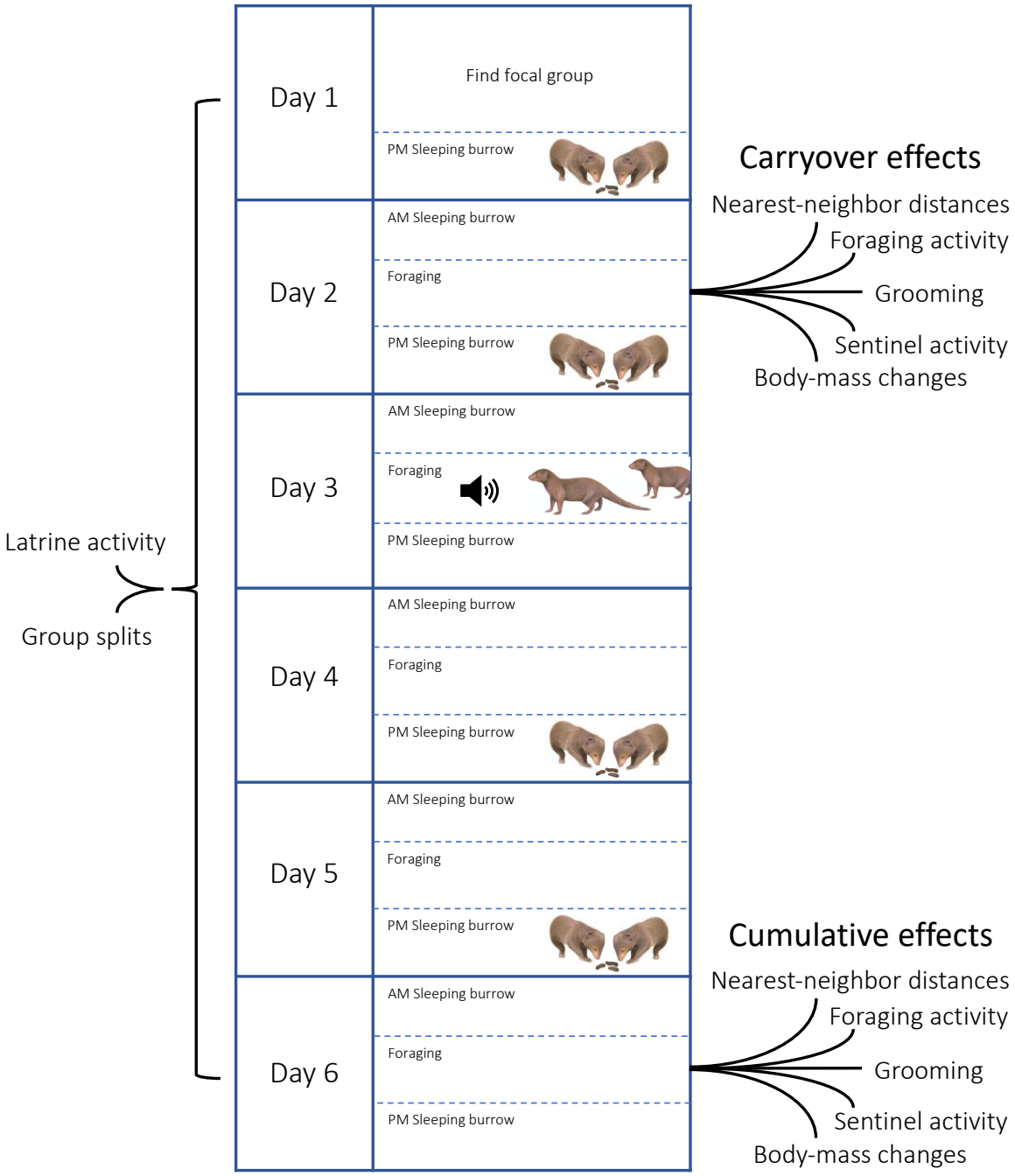

Figure 4.1 Illustration of a typical treatment week. In the experiment, each group (N=7) received two week-long treatments: an Intrusion week where the faecal presentations and call playback simulated the presence of a rival group, and a Control week where herbivore faeces and calls were used on an equivalent schedule. Data collection on Day 2 was used to investigate the carryover effects after the first simulated intrusion on Day 1, whilst data collected on Day 6 was used to investigate the cumulative effects after experiencing repeated simulated intrusions.

Within-group affiliation is one of the most commonly considered responses when assessing the immediate behavioural consequences of outgroup conflict (Payne et al. 2003; Radford 2008*b*; Bruintjes et al. 2016; Birch et al. 2019; Braga Goncalves and Radford 2019; Morris-Drake et al. 2019; Mirville et al. 2020). In dwarf mongooses, affiliation is displayed through allogrooming (Kern and Radford 2018; Morris-Drake et al. 2019) so we recorded grooming bouts between adults *ad libitum* when the group was foraging during the day. In our experiment, grooming behaviour was significantly affected by treatment the day after the first simulated intrusion: a greater proportion of time was spent grooming on Day 2 of Intrusion weeks compared to Control weeks (linear mixed model (LMM): χ^2=8.694, df=1, P=0.003; Table 4.1a; Figure 4.2a). This grooming difference was the result of both a greater frequency of grooming bouts (treatment: χ^2=6.353, df=1, P=0.012; Table 4.1b) and a longer mean bout duration, especially in males (treatment*sex interaction: χ^2=4.751, df=1, P=0.029; Table 4.1c). Inter-individual differences in grooming responses became more apparent following multiple simulated intrusions: whilst both dominants and subordinates spent a greater proportion of time grooming on Day 6 of Intrusion weeks compared to Control weeks, the difference was larger for subordinates (treatment*dominance interaction: χ^2=5.081, df=1, P=0.024; Table 4.2a). Similarly, the difference in the proportion of time grooming was greater for males than females, although this effect was not statistically significant (χ^2=3.103, df=1, P=0.078; Table 4.2a). As on Day 2, the treatment-based grooming differences were a consequence of both a greater grooming frequency (χ^2=7.704, df=1, P=0.005; Table 4.2b) and longer bout durations (treatment*sex: χ^2=5.501, df=1, P=0.019; treatment*dominance: χ^2=4.305, df=1, P=0.038; Table 4.2c; Figure 4.2b,c). Increased affiliation could be driven proximally by conflict-induced stress; giving and receiving grooming can reduce anxiety (von Holst 1998; Aureli et al. 1999; Aureli and Yates 2010). Discovery of rival cues could lead to increased anxiety for multiple reasons: for instance, intruders could threaten the positions of certain group members, encountering faecal deposits could lead to uncertainty over the rival group's current location and their recent presence could elevate the likelihood of a contest arising (Mares et al. 2011; Morris-Drake et al. 2019). Functionally, increased affiliation could incentivise future help in signalling or adversarial interactions with outsiders (Radford 2011; Arseneau-Robar et al. 2016; Radford et al. 2016).

Table 4.1 Output from LMMs investigating the grooming behaviour of adult individuals on Day 2: (a) log10-transformed proportion of time grooming; (b) log-transformed rate of grooming bouts; and (c) squareroot-transformed mean grooming-bout duration. All models included treatment, sex, dominance status and the interaction between treatment and sex and treatment and dominance status as fixed effects. Individual ID was nested within Group ID as random effects. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Proportion of time spent grooming					
Random effects	*Group ID*	0.230			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	-2.861±0.107			
	Treatment	**0.293±0.096**	**1**	**8.694**	**0.003**
Removed effects	Treatment:Status		1	0.043	0.836
	Treatment:Sex		1	2.858	0.091
	Status		1	0.012	0.913
	Sex		1	1.032	0.310
(b) Rate of grooming bouts					
Random effects	*Group ID*	0.280			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	-5.616±0.141			
	Treatment	**0.364±0.144**	**1**	**6.353**	**0.012**
Removed effects	Treatment:Sex		1	<0.001	0.982
	Treatment:Status		1	0.021	0.884
	Status		1	0.799	0.371
	Sex		1	2.059	0.151
(c) Mean grooming-bout duration					
Random effects	*Group ID*	1.902			
	Individual ID in Group ID	<0.001			
Minimal model	(Intercept)	5.671±0.865			
	Treatment	-0.333±0.758			
	Sex	-0.798±0.660			
	Treatment:Sex	**2.178±1.001**	**1**	**4.751**	**0.029**
Removed effects	Treatment:Status		1	<0.001	0.994
	Status		1	0.150	0.699

Table 4.2 Output from LMMs investigating the grooming behaviour of adult individuals on Day 6: (a) log10-transformed proportion of time grooming; (b) log-transformed rate of grooming bouts; and (c) log-transformed mean grooming-bout duration. All models included treatment, sex, dominance status and the interaction between treatment and sex and treatment and dominance status as fixed effects. Individual ID was nested within Group ID as random effects. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Proportion of time spent grooming					
Random effects	*Group ID*	0.000			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	-2.509±0.095			
	Treatment	0.118±0.132			
	Status	-0.616±0.120			
	Treatment:Status	**0.364±0.163**	**1**	**4.973**	**0.029**
Removed effects	Treatment:Sex		1	3.103	0.078
	Sex		1	0.648	0.421
(b) Rate of grooming bouts					
Random effects	*Group ID*	0.114			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	-5.096±0.131			
	Treatment	**0.357±0.125**	**1**	**7.704**	**0.006**
	Status	**-0.633±0.131**	**1**	**18.844**	**<0.001**
Removed effects	Treatment:Sex		1	0.016	0.901
	Treatment:Status		1	0.798	0.372
	Sex		1	1.686	0.194
(c) Mean grooming-bout duration					
Random effects	*Group ID*	0.103			
	Individual ID in Group ID	<0.001			
Minimal model	(Intercept)	3.510±0.201			
	Treatment	-0.257±0.268			
	Dominance	-0.670±0.213			
	Sex	-0.339±0.206			
	Treatment:Status	**0.601±0.289**	**1**	**4.305**	**0.038**
	Treatment:Sex	**0.633±0.276**	**1**	**5.501**	**0.019**

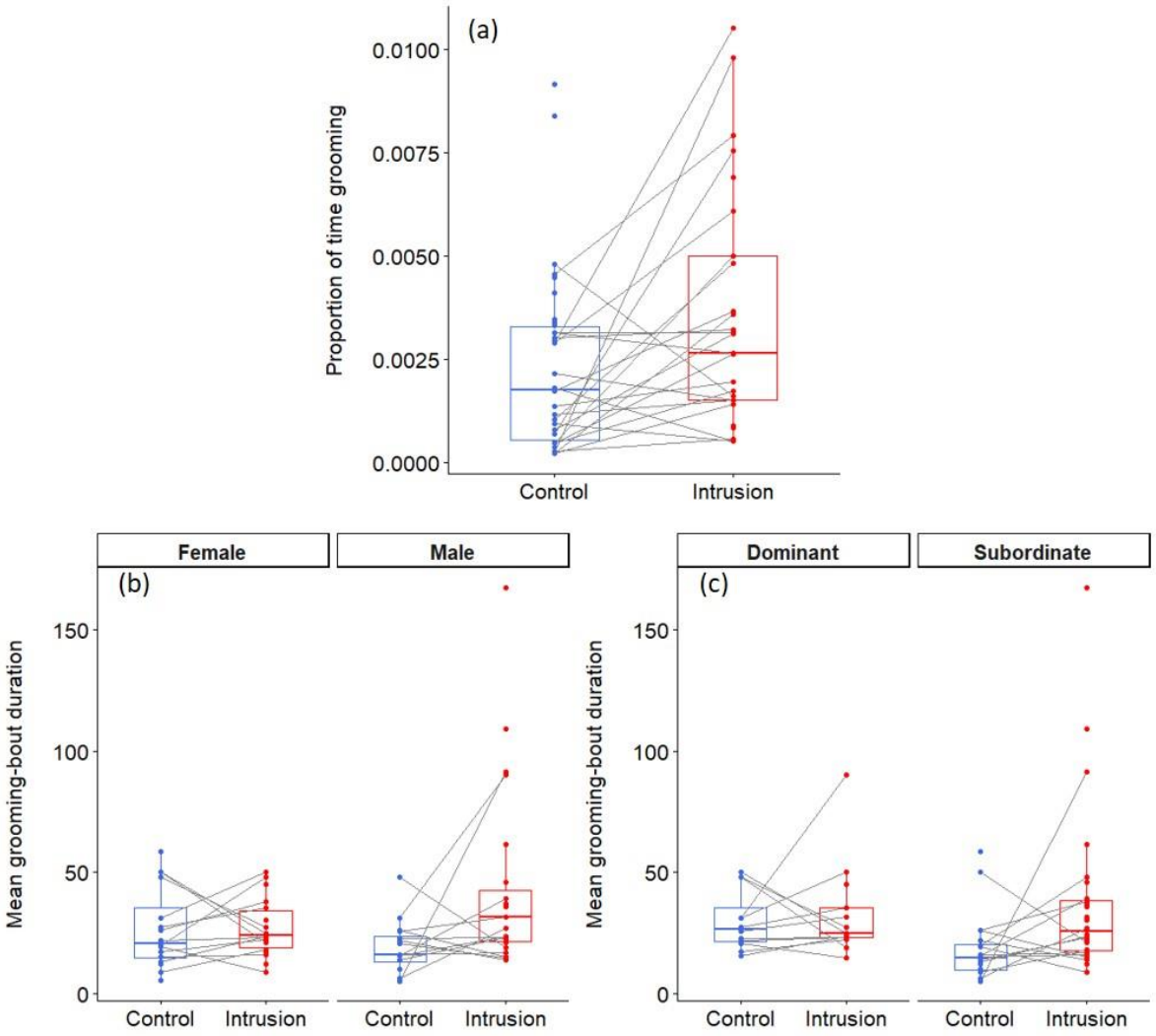

Figure 4.2 Effect of treatment week (Control: herbivore; Intrusion: rival group) on dwarf mongoose grooming behaviour. On Day 2 of Intrusion weeks, the day after the first simulated intrusion, adult individuals spent a greater proportion of time grooming compared to Control weeks (a). On Day 6 of Intrusion weeks, after repeated simulated intrusions, grooming bouts were longer (in seconds) than in Control weeks but the effect was more pronounced for males than females (b) and for subordinates than dominants (c). Shown in all panels are values for each individual separately, with grey lines connecting data from the same individuals; orphan points, where an individual only groomed in one treatment, are also plotted. In (a), N=67 observations from 44 individuals in seven groups; in (b,c), N=73 observations from 47 individuals in seven groups. Boxplots indicate the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range.

Recently, research into the behavioural consequences of outgroup threats has expanded beyond a focus on within-group interactions to consideration of individual foraging and vigilance decisions (Morris-Drake et al. 2019). Throughout the day, dwarf mongooses make constant decisions relating to foraging (e.g. how much time to spend foraging and how close to forage to groupmates; Kern and Radford, in revision) and vigilance (e.g. whether to act as a sentinel; Kern and Radford 2014, 2017). We therefore conducted scan-samples every 15 min during the day to record whether the group was foraging, and scan-samples every 30 min to record whether a sentinel was present and to estimate the distance between foraging nearest-neighbours. On Day 2 of our experiment, there was no significant difference between Control and Intrusion weeks in the amount of group foraging activity (proportion of 15-min scan-samples; Wilcoxon signed-ranks test: Z=1.363, N=7, P=0.213; Figure 4.3a), the amount of sentinel behaviour (proportion of 30-min scan-samples; generalised linear mixed model (GLMM): χ^2=0.015, df=1, P=0.903; Table 4.3a; Figure 4.3b) and the distance between nearest-neighbours when foraging (LMM: χ^2=2.415, df=1, P= 0.120; Table 4.3b; Figure 4.3c). However, on Day 6, there was significantly less group foraging activity (Wilcoxon signed-ranks test: Z=2.366, N=7, P=0.015; Figure 4.3a), a greater amount of sentinel activity, although the result was not statistically significant (GLMM: χ^2=2.994, df=1, P=0.084; Table 4.3c; Figure 4.3b), and individuals foraged significantly closer to other group members (LMM: χ^2=4.524, df=1, P=0.033; Table 4.3d; Figure 4.3c) in Intrusion weeks (when there had been prolonged rival-group exposure) compared to Control weeks. The Day 6 treatment difference for nearest-neighbour distances did not differ significantly between dominants and subordinates or between males and females (Table 4.3d). More sentinel behaviour could reflect an attempt to gain additional information about the intergroup threat, for which there has been no visual confirmation (Morris-Drake et al. 2019). The reduction in foraging activity likely reflects trade-offs with other behaviours, such as moving, latrining, grooming and vigilance, which ultimately reduce the time available for foraging (Hollén et al. 2008; Crofoot 2013; Mirville et al. 2020). Individuals may choose to forage in closer proximity to groupmates if that leads to a reduction in conflict-induced anxiety (Verbeek and de Waal 1997; Mallavarapu et al. 2006) or enhances the likelihood of support were an intergroup contest to arise (Morris-Drake et al. 2019).

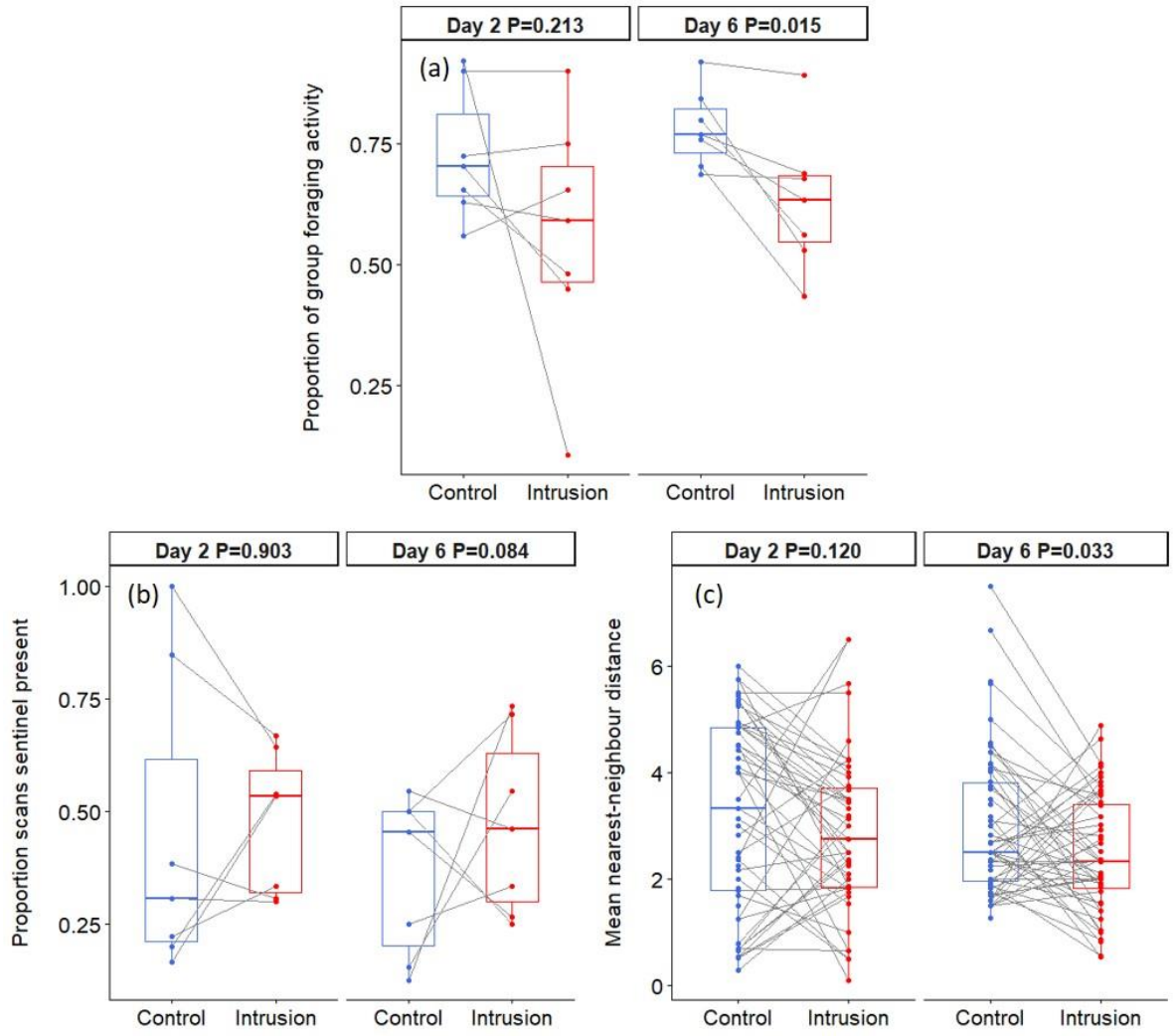

Figure 4.3 Effect of treatment week (Control: herbivore; Intrusion: rival group) on dwarf mongoose foraging and sentinel activity. On Day 6 of Intrusion weeks, after repeated simulated intrusions, there was a reduction in foraging activity (a), an increase in sentinel activity (b) and a reduction in nearest-neighbour distances (in metres) (c) compared to Control weeks; these effects were not apparent on Day 2. Shown in (a,b) are values for each group (N=7) and in (c) values for each individual, with grey lines connecting data from the same groups and individuals; orphan points, where an individual only has a value in one treatment, are also plotted in (c). In (c), N=100 observations from 53 individuals in seven groups on Day 2 and N=105 observations from 54 individuals in seven groups on Day 6. Boxplots indicate the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range.

Table 4.3 Output from GLMMs (binomial error distribution and logit-link function) investigating the likelihood that an adult individual was acting as a sentinel during a scan-sample on (a) Day 2 and (c) Day 6 of trial weeks. Both models included treatment, wind, habitat and group size as fixed effects, with Group ID as a random effect. Model outputs from LMMs investigating the squareroot-transformed nearest-neighbour foraging distances of adult individuals on (b) Day 2 and (d) Day 6 of trial weeks also presented. These models contained treatment, sex, dominance status, and the interactions between treatment and sex and treatment and dominance status as fixed effects; Individual ID was nested within Group ID as random effects. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Sentinel presence on Day 2					
Random effects	*Group ID*	0.544			
Minimal model	(Intercept)	0.263			
	Wind	**-0.536±0.245**	**1**	**4.757**	**0.029**
Removed effects	Habitat		2	0.061	0.900
	Treatment		1	0.015	0.903
	Group size		1	0.017	0.895
(b) Nearest-neighbour distance on Day 2					
Random effects	*Group ID*	0.330			
	Individual ID in Group	0.000			
Minimal model	(Intercept)	1.657±0.130			
Removed effects	Treatment:Sex		1	0.044	0.834
	Treatment:Status		1	0.983	0.322
	Sex		1	0.002	0.961
	Status		1	0.699	0.403
	Treatment		1	2.415	0.120
(c) Sentinel presence on Day 6					
Random effects	*Group ID*	0.130			
Minimal model	(Intercept)	0.127			
Removed effects	Group size		1	0.224	0.636
	Wind		1	2.359	0.125
	Habitat		2	3.510	0.173
	Treatment		1	2.994	0.084
(d) Nearest-neighbour distance on Day 6					
Random effects	*Group ID*	0.261			
	Individual ID in Group	0.000			
Minimal model	(Intercept)	1.623±0.107			
	Treatment	**-0.119±0.056**	**1**	**4.524**	**0.033**
Removed effects	Treatment:Status		1	0.137	0.711
	Treatment:Sex		1	0.374	0.541
	Status		1	0.584	0.445
	Sex		1	1.313	0.252

Reduced foraging, coupled with the possibility of chronic stress arising from a greater intergroup threat (Samuni et al. 2019), could have negative consequences for body mass (Wey et al. 2015). At the beginning and end of each trial week, we therefore weighed adults and independently foraging pups twice a day—once at their sleeping burrow in the morning (before leaving to start foraging) and again ca. 3 h into their morning foraging session—to determine body-mass changes. On Day 2, the body-mass change for adults (LMM: χ^2=0.042, df=1, P=0.840; Table 4.4a; Figure 4.4a) and independently foraging pups (χ^2=1.934, df=1, P=0.164; Table 4.4b; Figure 4.4b) did not differ significantly between Intrusion and Control weeks. However, by Day 6, both adults (χ^2=4.095, df=1, P=0.043; Table 4.4c; Figure 4.4a) and independently foraging pups (χ^2=4.901, df=1, P=0.027; Table 4.4d; Figure 4.4b) were putting on significantly less body mass in Intrusion weeks compared to Control weeks. There was no significant difference between adult individuals of different dominance status and sex in this Day 6 treatment effect (Table 4.4c). A sustained decline in body mass during periods of intense intergroup pressure could have fitness consequences, increasing the vulnerability of individuals to predation and disease (Vuarin et al. 2019). In addition, since many cooperative behaviours, such as babysitting, sentinel duty, offspring feeding and territorial defence, are state dependent (Clutton-Brock et al. 2003; Bruintjes et al. 2010; Arbon et al. 2020), individuals in poorer body condition might invest less in these activities with negative consequences for groupmates.

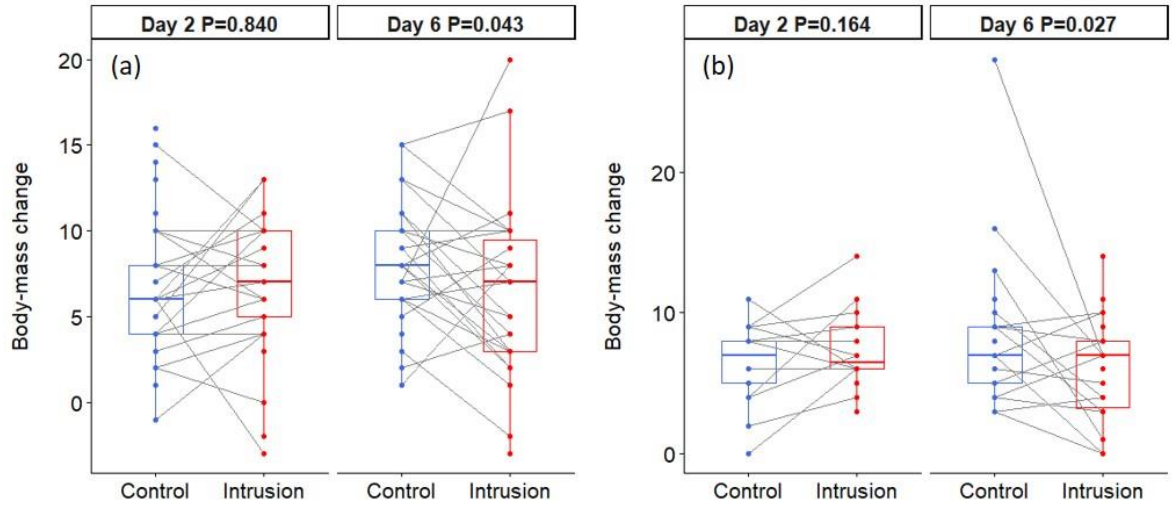

Figure 4.4 Effect of treatment week (Control: herbivore; Intrusion: rival group) on dwarf mongoose body-mass changes (in grams). On Day 6 of Intrusion weeks, after repeated simulated intrusions, adults (a) and independently foraging pups (b) were putting on less body mass compared to Control weeks; these effects were not apparent on Day 2. Shown are values for each individual separately, with grey lines connecting data from the same individuals; orphan points, where an individual only has a value in one treatment, are also plotted. In (a), N=62 observations from 39 individuals in seven groups on Day 2 and N=68 observations from 39 individuals in seven groups on Day 6. In (b), N=36 observations from 24 individuals in seven groups on Day 2 and N=43 observations from 26 individuals in seven groups on Day 6. Boxplots indicate the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range.

Table 4.4 Output from LMMs investigating body-mass changes for adults and squareroot-transformed body-mass changes for independently foraging pups on (a,b) Day 2 and (c,d) Day 6 of trial weeks. All models included treatment, sex and the interaction between treatment and sex as fixed effects; adult models also included dominance status and the interaction between treatment and dominance status as fixed effects. Individual ID was nested within Group ID as random effects. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	χ^2	P
(a) Change in adult body mass on Day 2					
Random effects	*Group ID*	0.746			
	Individual ID in Group ID	2.533			
Minimal model	(Intercept)	6.877±0.629			
Removed effects	Treatment:Status		1	0.020	0.888
	Treatment:Sex		1	1.471	0.225
	Status		1	0.057	0.811
	Treatment		1	0.041	0.840
	Sex		1	1.598	0.206
(b) Change in pup body mass on Day 2					
Random effects	*Group ID*	0.243			
	Individual ID in Group ID	0.173			
Minimal model	(Intercept)	2.544±0.145			
Removed effects	Treatment:Sex		1	2.620	0.106
	Sex		1	0.045	0.833
	Treatment		1	1.934	0.164
(c) Change in adult body mass on Day 6					
Random effects	*Group ID*	1.478			
	Individual ID in Group ID	2.018			
Minimal model	(Intercept)	8.092±0.879			
	Treatment	**-1.720±0.832**	**1**	**4.095**	**0.043**
Removed effects	Treatment:Sex		1	0.052	0.820
	Treatment:Status		1	0.090	0.764
	Sex		1	0.105	0.746
	Status		1	1.813	0.178
(d) Change in pup body mass on Day 6					
Random effects	*Group ID*	0.602			
	Individual ID in Group ID	0.000			
Minimal model	(Intercept)	2.925±0.296			
	Treatment	**-0.566±0.250**	**1**	**4.901**	**0.027**
Removed effects	Treatment:Sex		1	0.035	0.851
	Sex		1	0.004	0.952

By monitoring groups over the course of a whole trial week, we could also gain sufficient data to consider treatment effects on relatively rare group-level behaviours. One aspect of dwarf mongoose territorial defence is the depositing of scent-marks (urine, faeces, cheek-gland and anal-gland secretions) at communal latrines (Rasa 1973*c*; Christensen et al. 2016). In our experiment, groups spent a significantly greater proportion of time latrining during Intrusion weeks compared to Control weeks (Wilcoxon signed-ranks test: Z=2.028, N=7, P=0.046; Figure 4.5a). This was the result of a greater rate of latrining (Z=2.197, N=7, P=0.032), not an increase in the mean latrine duration (Z=0.676, N=7, P=0.572). Since group members often leave the main foraging party to latrine (personal observation), we also analysed the rate of group splits during trial weeks. Group splitting rate was greater in Intrusion weeks compared to Control weeks, although the result was not statistically significant (Z=1.859, N=7, P=0.076; Figure 4.5b). When under threat from rival groups, increasing advertisement of territory ownership may help to establish group dominance and thus increase the likelihood of resource retention (Amrhein and Erne 2006; Benedict et al. 2012). The tendency for an enhanced rate of group fission contrasts with work on green woodhoopoes and chimpanzees, where groups were less likely to split up during and after intergroup contests (Radford and Fawcett 2014; Samuni et al. 2017). Due to the benefits of collective defence in group-living species, group splits could have negative consequences for the group if it means members are absent when an intergroup contest arises (Langergraber et al. 2017).

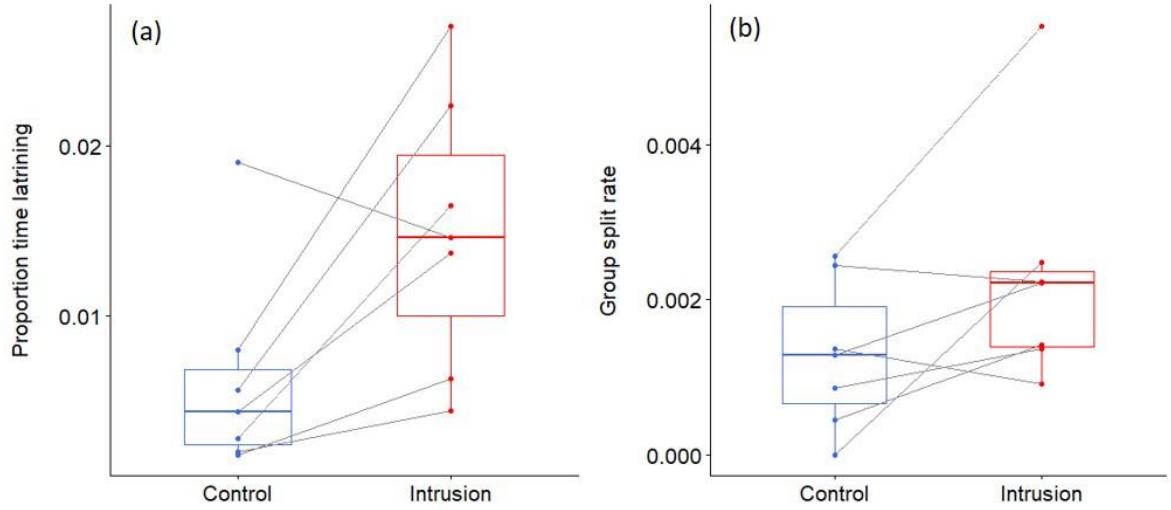

Figure 4.5 Effect of treatment week (Control: herbivore; Intrusion: rival group) on dwarf mongoose group-level activities. In Intrusion weeks, there was a greater proportion of time spent latrining (a) and more group splits (b) than in Control weeks. Shown are values for each group separately (N=7), with grey lines connecting data from the same groups. Boxplots indicate the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range.

4.4 Discussion

We provide strong experimental evidence for carryover and cumulative effects of intergroup conflict on within-group behaviour in dwarf mongooses. By looking beyond the immediate aftermath, we expand on previous research looking at the short-term behavioural implications of outgroup conflict in two main ways. First, we demonstrate that exposure to a single simulated rival-group intrusion can have a carryover effect into the following day; compared to their behaviour in Control weeks, dwarf mongooses invested more in grooming their groupmates on Day 2 of Intrusion weeks. Second, we show that exposure to repeated rival-group intrusions can lead to cumulative effects; by Day 6 of the Intrusion week, inter-individual differences in elevated grooming behaviour were more pronounced, foraging activity was reduced, foragers were in closer proximity to one another and individuals were putting on less body mass compared to Control weeks. In addition, groups spent more time marking their territories and showed a tendency to fission more often in Intrusion compared to Control weeks. Taken together, these findings provide the first field-based experimental evidence for longer-term changes in within-group behaviour after a period of elevated intergroup threat.

The increased grooming on Day 2 of Intrusion weeks was in-line with our prediction that there would be some lasting changes to individual behaviour after a single simulated intrusion. One explanation for increased grooming in the immediate aftermath of intergroup conflict is that GC levels are elevated (Aureli and Yates 2010; Wittig et al. 2016), but this is unlikely to explain the carryover effect. After a stressful stimulus, it is common for GCs to return from a peak to baseline within a couple of hours, although the more stressful the stimulus the longer it takes; there is some evidence that circulating GCs can remain elevated for up to 24 hours (Øverli et al. 1999). A single intergroup faecal presentation is unlikely to induce an intense stress response, especially since the presentation was in the evening of Day 1 and the grooming data were collected during Day 2. Moreover, if the carryover effect on grooming was due to a sustained GC response, we would expect to see other behavioural changes on Day 2 but we found no increase in sentinel activity or a reduction in nearest-neighbour foraging distance; results which were apparent in the hour after a simulated intergroup threat, when GCs are likely elevated (Morris-Drake et al. 2019). Instead, there could be a functional explanation for the increase in grooming on Day 2. Whilst delayed rewarding is known to occur in this species (Kern and Radford 2018), rewarding is unlikely to be relevant here as there was no intergroup contest that required involvement on Day 1. Rather, the increased grooming could be pre-emptive affiliation to increase groupmate participation in future contests (Radford 2011; Samuni et al. 2020), especially if the likelihood of a confrontation arising is greater having recently discovered fresh cues to the presence of a rival group. Data from vervet monkeys (*Chlorocebus pygerythrus*) shows that females

can influence subsequent male participation during extended intergroup encounters by grooming them (Arseneau-Robar et al. 2016), but further work is needed to determine whether grooming can be used to promote participation in future contests that occur hours or days later.

Also as predicted, we found that repeated exposure to intergroup threats over the course of a week resulted in greater behavioural changes than a single exposure; there were stronger treatment differences on Day 6 than Day 2. A possible proximate explanation relates to the influence of elevated GCs. Unlike on Day 2, where any stimulus-induced increase in GCs from the previous evening should have subsided (see paragraph above), the repeated discovery of cues from a rival group could lead to a build-up in GCs and chronic stress (McEwen 1998; McEwen and Wingfield 2003; Romero 2004). Increased grooming, foraging closer to other individuals and increased sentinel behaviour could all help to reduce anxiety (Bednekoff 1997; Mallavarapu et al. 2006; Aureli and Yates 2010). The reduction in body-mass gain could also be a direct effect of elevated GCs (McEwen 2017), alongside an indirect effect of greater investment in non-foraging related activities (grooming, sentinel, latrining). From a functional perspective, the demonstrated cumulative effects provide evidence for increased cooperation during periods of heightened intergroup conflict; findings which are in-line with previous observational studies reporting a positive correlation between outgroup interactions and various measures of in-group cohesion (Radford 2008*a*; Samuni et al. 2020), along with empirical work focussing on the immediate post-contest period (Radford 2008*b*; Bruintjes et al. 2016; Mirville et al. 2020). Dwarf mongoose cooperative behaviours such as grooming, latrining and sentinel activity all increased during Intrusion weeks compared to Control weeks and these behavioural changes occurred outside the immediate post-conflict period; these findings lend support to the idea that within-group cooperation should increase when the outgroup threat is greatest (Alexander and Bargia 1978; Choi and Bowles 2007; Bowles 2009).

We found evidence for intragroup variation in grooming responses to intergroup threats. The differences in individual grooming behaviour were more prominent on Day 6 than Day 2, after the dwarf mongooses had experienced evidence of intergroup threats for five consecutive days. Asymmetries in affiliative behaviour depending on individual characteristics have been reported in other nonhuman species both during and in the immediate aftermath of outgroup interactions (Radford 2008*a*, 2008*b*; Arseneau-Robar et al. 2016; Bruintjes et al. 2016; Braga Goncalves and Radford 2019). However, prior work on this study population did not find any differences in grooming based on dominance status or sex following a single simulated intergroup threat (Morris-Drake et al. 2019). Instead, differences in dwarf mongooses seem to emerge after a build-up in intergroup threat

level, likely because the perceived threat to particular individuals is greater after repeated simulated intrusions. Against expectations, the increase in grooming behaviour was greater for males compared to females and subordinates compared to dominants. Although we do not know how participation in defence differs among dwarf mongooses, males of many species contribute more than females (Fashing 2001; Majolo et al. 2005; Kitchen and Beehner 2007) and, for cooperatively breeding species, subordinate helpers often participate more than dominant group members (Cant et al. 2002; Radford 2003). Another possible reason for the differences we observed involves the stimuli we presented. Our rival faecal presentations and call playbacks were made up of deposits and calls from four adult individuals. In dwarf mongooses, males are the dispersing sex and often leave in a coalition of roving individuals to take over breeding or higher-ranked subordinate positions (Rood 1987). Therefore, it is possible that the stimuli were interpreted as a group of roving individuals attempting to join a new group. In this case, it is likely that males would perceive a greater threat as changes in rank would be more likely to occur in this sex. Our individual-based results add to a growing body of evidence that demonstrates how group heterogeneity leads to diverging behavioural consequences when exposed to intergroup threats and highlights the importance of considering intragroup variation in the study of outgroup conflict.

Overall, our results suggest that intergroup conflict can have longer-lasting behavioural effects than previously documented, either through carryover from single events or as a consequence of the cumulative build-up of threat. Whilst it is possible that even stronger responses might have been found if focal groups had encountered rival mongooses, the potential presence of rivals (as indicated by faecal presentations and call playbacks) was sufficient to generate at least some behavioural changes. This also showcases the value of such experimental methods, which are feasible in natural conditions and do not require the presentation of caged live conspecifics, a method that is likely to cause large stress to the presented individuals and raise ethical questions. Future studies need to move beyond behavioural responses and measure fitness consequences directly; to investigate how cumulative outgroups threats can impair, for example, immune function and growth (Sapolsky et al. 2000) and, ultimately, impact survival and reproductive success (Thompson et al. 2017; Lemoine et al. 2020*a*).

4.5 Methods

4.5.1 Study Site and Population

We conducted this study at the Dwarf Mongoose Research Project (DMRP), which is based on a private game reserve in South Africa (Sorabi Rock Lodge, Limpopo Province, 24° 11’S, 30° 46’E); full details of

the study site are provided in Kern and Radford 2013. We carried out the experimental manipulations between June and September 2018 (the non-breeding season) on seven wild dwarf mongoose groups (mean group size: 13.4, range: 8–21). Groups were habituated to the close presence of observers (<5 m) and individuals were trained to climb onto electronic weighing scales for assessment of body mass in exchange for a small amount of hard-boiled egg (Kern and Radford 2017). All individuals in the population were of known sex and could be individually identified by natural features (stumpy tails/scars) or dye marks on their fur (blond hair dye applied using an elongated paintbrush). We classed individuals as adults once they reached 12 months of age and pups were deemed to be foraging independently once they began foraging with the group (Kern et al. 2016). The dominance status (dominant breeding pair or subordinate helpers) of all adult group members was known, with the dominant breeding pair identified by observations of targeted aggression and foraging displacements (Rasa 1977; Kern and Radford 2013).

4.5.2 Simulated Intrusions

The use of dwarf mongoose and herbivore faecal presentations followed the general protocol of Morris-Drake et al. (2019). We conducted faecal presentations most evenings (Days 1–5) in each treatment week. For Intrusion weeks, we collected fresh dwarf mongoose faeces from relevant groups (non-neighbouring groups that did not share any territorial boundaries with the focal groups); for Control weeks, we collected fresh giraffe (*Giraffa camelopardalis giraffe*) faecal pellets (similar in diameter to dwarf mongoose faeces). Non-neighbouring groups were chosen for our rival intrusions as they are encountered naturally in the wild (Rasa 1987; Sharpe et al. 2015) and allowed us to avoid restrictions associated with using neighbouring group stimuli; namely, only being able to run experimental trials in certain areas of a territory (i.e. the area that overlaps with that particular neighbour). Each faecal deposit was placed in a separate airtight zip-lock bag and stored in a thermos flask on ice whilst in the field. Samples were transferred to a -20°C freezer on return to base (mean±SE duration between collection and placement in freezer: 4.47±0.01 h, range: 0.05–10.47 h). We used samples in faecal presentations within one month of collection (mean±SE days between collection and presentation: 18.8±0.7 days, range: 1–32 days). Prior to starting an Intrusion week, we organised the samples from the relevant group so that each faecal presentation comprised one deposit per day from four different adult group members, including at least one dominant individual. Different faecal samples were used on each presentation day in both treatments.

The use of dwarf mongoose and herbivore call playbacks also followed the general protocol of Morris-Drake et al. (2019). We conducted one playback (rival-group or control) mid-week (Day 3 or

4) in each treatment for the purpose of maintaining rival-group or herbivore exposure rather than data collection. We constructed playback stimuli from original sound recordings made using a handheld Sennheiser ME66 directional microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK), coupled with a Marantz PMD660 solid-state recorder (Marantz America, Mahwah, NJ). Recordings had a sampling rate of 48 kHz, a 16-bit resolution, were saved in wav format and were always collected when weather conditions were calm. For Intrusion weeks, we made recordings of close and lost calls opportunistically during observation sessions with the appropriate groups. Close calls (low-pitched vocalisations) are produced continuously when dwarf mongooses are foraging and moving (Kern and Radford 2013; Sharpe et al. 2013), whilst lost calls (high-pitched vocalisations) are given in a range of circumstances, including coordinating lost group members and group movement, as well as during intergroup interactions (IGIs) (Rubow et al. 2017*b*, 2018). These calls were used to simulate the nearby presence of a rival-group and the potential of an imminent IGI. We obtained close-call recordings from four adult group members (either one dominant and three subordinates, or both dominants and two subordinates) from 0.5 to 3 m, and recorded lost calls from two adult group members from 1 to 10 m. We measured the maximum sound-pressure level (SPLA) of these two call types using a HandyMAN TEK 1345 sound-level meter (Metrel UK Ltd., Normanton, UK). For Control weeks, we recorded zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) sounds from close to the main lodge at the study site; the microphone was attached to a tree 10 m from an artificial feeding area and left to record for 1 h.

We constructed five-minute rival-group and control playback tracks in Audacity (version 2.1.3). For the rival-group tracks used in Intrusion weeks, close and lost calls with good signal-to-noise ratios were extracted from original sound recordings. We then created each track following a five-step process. (1) Four different close-call sequences were constructed, with each sequence comprising four unique close calls (one per individual). (2) These sequences were randomly selected and inserted into a 12 s block of ambient sound; this step was repeated five times. (3) The five 12 s blocks were stitched together in a random order to create a 1 min sequence. (4) Five close calls were randomly removed to create a close-call rate of 75 calls per minute (natural rate of four dwarf mongooses; Sharpe et al. 2013), and four lost calls (two per individual, alternating between them) were randomly added to the first 30 s of the 1 min block, resulting in a rate of four calls per minute (this falls within their natural range; Rubow et al. 2017*b*). (5) The 1 min call sequence was copied five times to produce a 5 min rival-group track. For the herbivore tracks used in Control weeks, we extracted zebra and wildebeest grunts and huffs with good signal-to-noise ratio from original recordings. We then created each track using

the same general process above (minus step 4), but each sequence in step 1 only included one herbivore sound so that when the five 12 s blocks were stitched together in step 3 the overall rate was 20 herbivore sounds per minute. For all playback tracks, we faded sounds in gradually to simulate an approach. Halfway into each track, the amplitude was 55 dB SPLA at 1 m for close calls and herbivore sounds and 60–65 dB SPLA at 1 m for lost calls; these were the natural volumes of dwarf mongoose close calls and lost calls, as determined by the sound-level recordings (see above). We constructed unique rival-group and control tracks for different groups.

4.5.2.1 Experimental protocol

We counterbalanced treatment order between groups as much as was possible; four groups received the Intrusion week first, whilst three received the Control week first. Our aim was to leave 2 weeks between treatments to the same group. Each experimental week comprised 3–5 faecal presentations on separate days throughout the week (Days 1–5) and one playback on either Day 3 or 4 (Figure 4.1). To compare dwarf mongoose behaviour after a single intrusion (Day 2) and repeated intrusions (Day 6), it was essential that each group received a faecal presentation on Days 1 and 5. It was also critical that the weather conditions were calm and there were no major group disturbances (IGIs, predatory attacks) during the afternoon/evening on Day 1 and 5, and all day on Day 2 and 6. We therefore had to abandon, and later repeat, three trial weeks because these conditions were not met. Natural IGIs that occurred on non-essential days (Days 3 and 4) could have influenced dwarf mongoose behaviour, but there was no significant difference in the likelihood of an IGI occurring in Intrusion and Control weeks (McNemar test: $\chi^2 = 0$, df=1, P=1).

We conducted faecal presentations at the evening sleeping burrow; burrows are regularly contested between groups (DMRP unpub. data). During the day, we stored the sample to be presented in the evening on ice in a thermos flask. When the group started getting ready to move to a sleeping site (indicated by an increase in the rate of close and movement calling), we removed the faecal sample from the thermos flask to defrost before the presentation. To reflect the natural situation whereby a rival group had deposited faeces at a burrow whilst the focal group had been away foraging, the observer moved ahead of the focal group and placed the relevant faecal sample near the sleeping burrow. Once the dwarf mongooses arrived at the sleeping burrow, we attracted the group to a location 2–5 m from the faecal presentation using a small amount of hard-boiled egg (as in Morris-Drake et al. 2019). On five occasions (never on Days 1 or 5), the group moved to a different sleeping burrow after the faeces had been encountered by the focal group. In these instances, we did not relocate the presentation; we always left the sample at the site where it was first presented.

We conducted playbacks on Day 3 or 4 of experimental weeks (depending on which day had the best weather forecast) when the group was foraging and there had been no natural alarm call or group disturbance (e.g. latrine event, snake mob) for at least 10 min. We played back tracks from an iPhone 4 (Apple Inc., Cupertino, California, USA) through a portable loudspeaker (Rokono B10, London, UK), which was concealed in vegetation. The mongooses were attracted to a location 5 m from the loudspeaker using a small amount of hard-boiled egg (as in Morris-Drake et al. 2019). Once 50% of the adults in the group were present, we started the relevant playback track (rival-group or control).

4.5.2.2 Data collection

To verify that rival-group faecal presentations induced an intergroup response as planned, we recorded to a Dictaphone (ICD-PX312, Sony, Sony Europe Limited, Surrey, UK) the immediate reactions to the first and last faecal presentation (Day 1 and Day 5 respectively) in each trial week. These reactions were the identity of all adult individuals that interacted with the deposit and the duration of all occasions that individuals sniffed the presentation (as in Morris-Drake et al. 2019). We started dictation once the mongooses were called to the faecal-presentation area (see above) and finished when they had moved below ground for the night or to a different burrow. We ran Wilcoxon signed-ranks tests in SPSS 24 (IBM Corp, 2016) to analyse the proportion of the group that interacted with the faeces and the total time spent sniffing the faeces for Day 1 and 5 separately. There was a significantly greater proportion of individuals interacting with the rival-group faeces compared to the control faeces on Day 1 (Wilcoxon signed-ranks test: $Z=2.207$, $N=7$, $P=0.031$), although the effect was dampened slightly by Day 5 ($Z=1.782$, $N=7$, $P=0.097$). However, the total time spent sniffing the faeces was significantly longer for rival-group faeces than control faeces on both Day 1 ($Z=2.366$, $N=7$, $P=0.015$) and Day 5 ($Z=2.197$, $N=7$, $P=0.033$).

To assess behavioural changes after exposure to a single rival-group intrusion and repeated intrusions, we conducted observations on Days 2 and 6 of each treatment week, following established DMRP protocols (Kern and Radford 2017, 2018). We recorded all behavioural data in a field notebook and later inputted these into an Excel spreadsheet. In the period between 50% of the group leaving the morning sleeping burrow and 50% arriving at the evening sleeping burrow, we collected data on grooming interactions, sentinel behaviour, nearest-foraging-neighbour distances and group foraging activity. Adult grooming interactions were collected from all-occurrence sampling and involved recording the identity of those involved and the duration of the bout (measured using a stopwatch)

(Kern and Radford 2018; Morris-Drake et al. 2019). Sentinel and nearest-neighbour foraging scan-samples were carried out every 30 min. Sentinel scan-samples entailed noting whether a sentinel was present, along with the habitat type that the group was foraging in (open, medium or dense) and the wind conditions (still, light breeze, strong). Sentinels were defined as individuals actively scanning their surroundings from an elevated post (termite mound, rock, tree)—feet at least 10 cm off the ground—whilst their groupmates were engaged in other activities (usually foraging) (Kern and Radford 2013, 2014). Foraging scan-samples involved estimating the distance (to the nearest 0.5 m) to the nearest neighbour for each identified adult group member in sight, with minimal observer movement to avoid disturbing foragers (Morris-Drake et al. 2019, Kern and Radford, in revision). A foraging-activity scan-sample was also carried out every 15 min to determine whether the majority of the group (>50%) was engaged in foraging behaviour. In addition to these behavioural data, we weighed individuals for assessment of body mass on Day 2 and Day 6. As many individuals as possible (adults and independently foraging pups) were weighed after emergence at the morning sleeping burrow and again after a 3-h foraging session. Individuals were enticed onto the electronic scales (Salter 1035 SSBKDR, Tonbridge, Kent, UK) using a small amount of hard-boiled egg as a reward (Kern and Radford 2017). We recorded body mass when scale readings were constant for at least 2 s.

Throughout each trial week, we also collected data *ad libitum* when the group engaged in any latrine behaviour; which is when group members leave scent-marks (urine, faeces, cheek-gland and anal-gland secretions) at communal sites (rocks, trees, termite mounds) around their territory (Rasa 1973*c*; Christensen et al. 2016). We recorded the occurrence and duration of each latrine event. We also noted the occurrence of group splits, which involve the main group dividing into sub-groups, usually after they have all left the morning sleeping burrow together. Individuals would either intentionally leave the main group (producing continuous movement calls in a particular direction) or would become lost as a by-product of foraging too far apart.

4.5.3 Data Analysis

All statistical tests were two-tailed and considered significant at $P<0.05$. We conducted parametric tests where data fitted the relevant assumptions of normality and homogeneity of variance. Transformations were conducted to achieve normality in some cases, otherwise we used non-parametric tests. For group-level analyses (foraging activity, latrining, group splits), we ran Wilcoxon signed-rank tests in SPSS 24 (IBM Corp, 2016). Since sample sizes were small (N=7 groups), we used the Monte Carlo resampling method (10,000 samples) to generate P-values. For individual-level analyses, when multiple factors needed to be taken into consideration, we conducted LMMs or

GLMMs (Bolker 2015) in RStudio 3.6.2 (R Core Team 2019) using the package lme4 (Bates et al. 2015). Mixed models combine fixed and random effects; incorporation of the latter avoids pseudoreplication by bringing our repeated-measures experimental design (repeated trials to the same group/individual in a group) into the model. In each analysis, we included fixed effects and two-way interactions of interest in the maximal model. We determined the minimal model by sequentially removing non-significant interactions followed by main fixed effects (using the drop1 function) until only effects that significantly improved the fit of the model were left. We assessed the significance of interactions and fixed effects by comparing a model including the effect of interest with a model excluding it and testing the change in deviance between the models with likelihood ratio tests (ANOVA model comparison), along with the Akaike Information Criterion (Crawley 2007; Bolker et al. 2009). We added non-significant effects individually back to the minimal model to obtain significance levels, whilst we obtained values for significant effects either by comparing the term with a null model or by comparing the full minimal model with each term removed individually. We checked the residuals of LMMs graphically to ensure that the data conformed to the assumptions of normality and homoscedasticity.

We used separate Gaussian LMMs to analyse the grooming behaviour of individuals on Day 2 (to determine carryover effects of single rival-group intrusions) and Day 6 (to determine cumulative effects of repeated rival-group intrusions) of each trial week. Grooming bouts of over 5 s in duration were considered and were classed as separate bouts when 10 s elapsed without any grooming (Kern and Radford 2018). We adopted a two-stage process. First, we analysed the proportion of time that individuals spent grooming (summed grooming durations for each individual divided by the day duration; defined as the duration between 50% of the group leaving the morning sleeping burrow and 50% of the group returning to an evening sleeping burrow). We then ran further LMMs to investigate whether the increase in proportion of time grooming was due to individuals grooming at a greater rate (number of grooming interactions each individual was involved in divided by the day duration) or for longer durations (mean bout duration of each individual).

We also used mixed models to analyse the Day 2 and Day 6 sentinel, nearest-neighbour and body-mass data. We used binomial GLMMs with a logit link function to analyse the likelihood of sentinel occurrence, where the dependent variable was whether a sentinel was present during the scan-sample (Yes or No). We used Gaussian LMMs to analyse the nearest-neighbour distances at the individual level. In this case, the distance to an individual's nearest-neighbour was the dependent variable. Distances were recorded in 0.5 m intervals, but when the distance between two individuals was recorded as less than 0.5 m it was rounded down to 0.1 for statistical analysis. We also used

Gaussian LMMs to analyse body-mass change during the morning observation session. We ran separate body-mass models for adults and for independent pups.

Chapter 5: Reproductive Consequences of Outgroup Conflict

Morris-Drake A., Kern J. M., Radford A. N. Reproductive consequences of outgroup conflict.

Contents of Chapter Five will be combined with additional data and analyses for later publication.

AMD co-designed the study, maintained the habituated study population, collated the data, carried out the data analysis, interpreted the results and drafted the manuscript; JMK established and maintained the habituated study population and helped interpret the results; ANR co-designed the study, advised on data analysis, helped interpret the results and commented on the manuscript.

5.1 Abstract

Outgroup conflict is prevalent in social species from primates to ants and an extensive literature exists on the contests that occur between rivals. In recent years, there has been increasing interest in the consequences of outgroup conflict, particularly behavioural changes in the aftermath of single interactions and how individual contests can affect fitness directly or indirectly. However, the cumulative pressure of outgroup threats may also potentially influence reproductive success. Here, we use long-term observational and reproductive data from a wild population of dwarf mongooses (*Helogale parvula*) to investigate how intergroup interactions (IGIs) might affect breeding and offspring survival. IGI rate did not significantly affect the number of litters produced in a season, the inter-litter interval or the number of pups that emerged from the burrow. However, IGI rate significantly correlated with pup survival in the three months post-emergence: contrary to predictions, groups experiencing a higher IGI rate had more pups (in absolute number and proportion of those emerging) surviving to three months. This positive relationship between IGI rate and pup survival is in direct contrast to that seen in the two other species studied, and suggests that the intensity of contests with conspecific outsiders may influence the reproductive impact of outgroup conflict.

5.2 Introduction

Conflict with conspecific outsiders is a prominent feature of life for many social species (Wilson and Wrangham 2003; Kitchen and Beehner 2007; Mares et al. 2012; Ridley 2012; Radford et al. 2016). Groups and their members can come into conflict with rivals for a variety of reasons. For instance, individuals may be attempting to increase reproductive opportunities, to take-over a breeding position or to transfer to a higher-ranking position (Mares et al. 2012; Ridley 2012; Bruintjes et al. 2016), whilst groups may be seeking to increase access to resources such as food and sleeping sites, or even whole territories (Wilson and Wrangham 2003; Mosser and Packer 2009; Mitani et al. 2010; Radford and Fawcett 2014). An extensive body of research exists on outgroup contests themselves, considering inter-individual differences in participation (e.g. sex and rank differences; Boydston et al. 2001; Fashing 2001; Majolo et al. 2005; Kitchen and Beehner 2007; Desjardins et al. 2008; Mirville et al. 2018*b*), the type of interaction (e.g. signalling exchanges or physical fighting; Radford 2003; Radford and Du Plessis 2004*b*; Rosenbaum et al. 2016; Mirville et al. 2018*a*), factors influencing the outcome (e.g. location and relative-group size; Crofoot et al. 2008; Batchelor and Briffa 2011; Furrer et al. 2011; Jordan et al. 2017; Strong et al. 2018) and the hormonal underpinnings (e.g. cortisol and oxytocin; Schoof and Jack 2013; Wittig et al. 2016; Samuni et al. 2017, 2019). More recently, there has been an increasing focus on the consequences of outgroup conflict (Radford et al. 2016; Thompson et al. 2017; Lemoine et al. 2020*a*).

To-date, the primary focus of research investigating the consequences of outgroup conflict has been the short-term (usually within 1 h) behavioural changes seen in the aftermath of interactions with outsiders or cues of their presence (Radford 2008*a*, 2008*b*; Bruintjes et al. 2016; Birch et al. 2019; Braga Goncalves and Radford 2019; Morris-Drake et al. 2019; Mirville et al. 2020). The most commonly considered responses have been within-group behavioural exchanges, such as affiliation (e.g. allogrooming in mammals, allopreening in birds or social contacts in ants and fish) and aggression. Studies across a range of taxa have found that outgroup threats can lead to increased within-group affiliation, for instance in: birds (Radford 2008*a*, 2008*b*), fish (Bruintjes et al. 2016), ants (Birch et al. 2019), mongooses (Morris-Drake et al. 2019) and primates (Mirville et al. 2020). Moreover, there is some evidence for a reduction in within-group aggression (Mirville et al. 2020; Preston et al. 2020; Samuni et al. 2020). Outgroup interactions have also been demonstrated to alter individual decisions about foraging and vigilance (Morris-Drake et al. 2019), as well as group movement and activity patterns (Crofoot 2013; Christensen et al. 2016; Seiler et al. 2018; Mirville et al. 2020; Yi et al. 2020). There is more-limited evidence that individual events could have longer-lasting behavioural consequences, with studies showing continued effects at the end of encounter days (Crofoot 2013;

Radford and Fawcett 2014; Dyble et al. 2019; Yi et al. 2020), and into the following day and week (Chapter 4). However, since outgroup conflict is viewed as a powerful selection pressure (Choi and Bowles 2007; Bowles 2009), what is ultimately required is investigation of fitness consequences.

The most obvious fitness consequences are those arising to individuals as a result of an outgroup contest. Participants could suffer immediate survival and reproductive costs, especially if a contest escalates to physical violence. Perhaps the most extreme example occurs in chimpanzees (*Pan troglodytes*), where males have been observered undertaking targeted raids into neighbouring territories, attacking and killing conspecifics (Goodall et al. 1979; Wilson et al. 2014). More commonly, mortality is a by-product of aggressive outgroup contests, as seen in many social species, for example: primates (Gros-Louis et al. 2003; Aureli et al. 2006; Rosenbaum et al. 2016), carnivores (Mosser and Packer 2009; Cassidy et al. 2015; Jordan et al. 2017; Thompson et al. 2017; Dyble et al. 2019), birds (Hannon et al. 1985) and insects (Batchelor and Briffa 2011; Rudolph and Mcentee 2016). Immediate reproductive costs could arise from outgroup contests if a dominant individual is usurped by an outsider and loses its breeding position (Packer and Pusey 1983; Doolan and Macdonald 1996; Fedigan 2003; Beehner and Bergman 2008) or if extra-group matings occur during the encounter and so dominant males lose paternity (Lazaro-Perea 2001; Cant et al. 2002; Nichols et al. 2015). Individual outgroup contests could also have delayed fitness consequences for both those involved and non-participants. For example, injured individuals might experience a subsequent increase in mortality risk or reduction in reproductive performance (Bernado and Agosta 2005; Krause et al. 2017). Incoming males might later kill existing young (infanticide) to bring females into oestrus sooner, which has clear negative repercussions for the reproductive success of the parents (Packer and Pusey 1983; Fedigan 2003; Beehner and Bergman 2008; van Belle et al. 2010). A new breeder could also evict existing group members who would subsequently suffer costs associated with being alone or in small splinter groups (Packer et al. 1988; Ridley et al. 2008; Young and Monfort 2009; Mares et al. 2012). Fitness consequences are not restricted to single outgroup contests, however; there is also the possibility of cumulative effects arising from multiple events across time.

In the wild, outgroup interactions occur on a repeated basis and so animal groups live in a 'landscape of fear', as is the case with predation (Creel and Christianson 2008). As with other stressors, an increase in outgroup threat level could result in chronic stress (Samuni et al. 2019), with direct costs for individual fitness. Chronic stress can influence mortality risk through a reduction in body condition (Pride 2005; Wey et al. 2015) and increased vulnerability to predation and disease (Romero et al. 2009; Vuarin et al. 2019). It can also have a negative effect on reproduction by, for example, reducing

breeding rates (Mileva et al. 2011; Dulude-de Broin et al. 2020), the number of young (Boonstra et al. 1998), offspring size (Dantzer et al. 2018) and offspring survival (Eriksen et al. 2015). Two studies have specifically considered the cumulative effect of intergroup conflict on reproductive success in the wild. In chimpanzees, high rival neighbour pressure decreased the probability of offspring survival during pregnancy and resulted in longer inter-birth intervals (Lemoine et al. 2020*a*). In banded mongooses (*Mungos mungo*), intergroup interactions (IGIs) decreased pup survival, with litters less likely to emerge if there had been a contest shortly after birth, but reduced the likelihood of abortion (Thompson et al. 2017). Chimpanzees and banded mongooses are rare examples of species in which there is frequent, lethal violence between groups (Johnstone et al. 2020). To further our understanding of the effects of outgroup conflict on reproductive success, we need additional studies in natural conditions that consider species with less violent outgroup tendencies.

Here, we used long-term data from a wild dwarf mongoose (*Helogale parvula*) population to investigate the potential effects of intergroup conflict on reproductive success. Dwarf mongooses are a cooperatively breeding species: the dominant pair monopolise reproduction over the breeding season (ca. September to March), whilst subordinate group members of both sexes help raise their offspring (Rasa 1977; Rood 1980); subordinate females occasionally breed at the same time as dominants (Creel and Waser 1991). Dominant females deliver up to three litters over the breeding season, with each litter containing up to six pups (Rood 1990). Group members cooperate to defend a shared territory from conspecific rivals (Rood 1983; Christensen et al. 2016). Territorial defence in dwarf mongooses involves scent-marking at communal latrines and engagement in IGIs when rival groups are encountered (Rasa 1973*c*). We focussed specifically on the effect that IGIs have on reproductive success as they are predicted to be a greater threat and thus a stronger stimulus for behavioural change than latrine behaviour. We predicted that groups which have a higher IGI rate would have fewer breeding attempts, longer inter-litter intervals and reduced pup survival.

5.3 Methods

5.3.1 Study Site and Population

The data used in this chapter were collected as part of a long-term study of wild dwarf mongooses on Sorabi Rock Lodge, a 400 ha private game reserve located in Limpopo Province, South Africa (24° 11'S, 30° 46'E); further details available in Kern and Radford (2013, 2014). The Dwarf Mongoose Research Project (DMRP) was established on the reserve in 2011 and has been running continuously since then. At any given time, up to eight mongoose groups are monitored. Each group has their own distinct territory and range in size from 2 to 24 individuals. Study groups are habituated to human presence

and can be observed on foot at <5 m, with individuals identifiable by unique dye-marks on their fur (applied with an elongated paintbrush) or distinct physical features such as scars (Kern and Radford 2013). Individuals are sexed by observation of ano-genital grooming (Kern et al. 2016), and adult individuals (those older than 12 months) are classified as either dominant (the male and female breeding pair) or subordinate (all remaining adults, who act as helpers) (Kern et al. 2016). Dominance is determined through observation of agonistic interactions, scent-marking and grooming (Rasa 1977; Kern and Radford 2013). Daily rainfall is recorded from a rain guage on the reserve.

5.3.2 Data Collection

The DMRP maintains a year-round field team of four researchers, comprising an in-field manager, postgraduate students and research assistants. Throughout my PhD, I have been responsible for the advertising, shortlisting, interviewing and organising of research assistants on the DMRP. In the field, each mongoose group is visited every week for 2–3 days at a time. Typically, an observer follows a group from its emergence at a sleeping refuge in the morning until it enters a sleeping refuge in the evening. The day is split into a morning and afternoon observation session. During these sessions, observers maintain habituation levels via their continued presence and daily weights sessions, re-apply dye-marks when they start to fade, track group movement with a GPS, and collect data on group size and composition, individual and group behaviour (e.g. sentinel activity, grooming and dominance interactions, nearest-foraging neighbours, latrine events and IGIs), body-mass and life-history events (e.g. pregnancies, births, emigrations, immigrations). Whilst being a part of the field team, researchers enter their data into a long-term database. Each month, the in-field project manager scans the data and amends any obvious mistakes, such as incorrect ID codes and group sizes, whilst preparing the data from that month to be sent to an official data manager. The data manager goes through each spreadsheet in detail, raising any queries that need input from field researchers and amending any mistakes (e.g. typos, data in incorrect cells, inconsistencies in data entry, duplicate entries, anomalies). I have personally contributed data from five field seasons: five months as a Research Assistant, six months as a Masters student, and 15 months from three seasons as a PhD student. I have also error-checked and maintained the long-term database for extensive periods.

To examine the relationship between IGIs and reproductive success, we used data collected from seven breeding seasons between 2012 and 2019 (data from one breeding season was discarded due to incomplete data collection). Interactions with conspecific outsiders were recorded *ad libitum* whenever they occurred. This included interactions of a focal group with lone dispersers (13 of 195 events, 6.7%), with coalitions of roving individuals (11 of 195 events, 5.6%) and with whole groups

(171 of 195 events, 87.7%). In dwarf mongooses, outgroup interactions range in intensity from signal exchanges (mainly visual and acoustic, 71 of 195 events, 36.4%) to physical encounters (124 of 195 events, 63.6%). The majority of these physical encounters involve aggressive chasing by some or all of the individuals in a group (77 of 124 events, 62.1%); encounters that escalate into further aggression such as fighting were rarer (47 of 124 events, 37.9%). We included all types of outgroup interaction (hereafter IGIs) in our analyses, regardless of who the interaction was with and whether it escalated to physical fighting, as all interactions incur at least some costs (Radford et al. 2016).

In each breeding season (ca. September to March), the pregnancy status of adult females was tracked by monitoring of body mass and visible anatomical signs; when pregnant, females exhibit swelling of the abdomen and nipples. The birth of a litter was identified by a sudden reduction in body mass, changes in the visible appearance of females and changes in group behaviour; once pups are born, subordinate individuals remain at the burrow to babysit whilst the rest of the group forage, and groups reliably return to the same burrow at the end of the day. Pup emergence was defined as the first time that pups were seen at the burrow entrance, having emerged by themselves; pups spend approximately their first three weeks being cared for in the burrow. An emerged pup was assumed to have died when it was not present during an observation session.

5.3.3 Data Analysis

To analyse the effect of IGIs on reproductive success in dwarf mongooses, we constructed linear mixed models (LMMs) and generalised linear mixed models (GLMMs) in RStudio 3.6.2 (R Core Team 2019) within the package lme4 (Bates et al. 2015). For all models, we included Group ID and Breeding Season as random effects to account for multiple litters from the same group and breeding season. Error distributions were chosen such that there were no obvious deviations from normality or homoscedasticity, checked by graphical examination of residual plots. There was also no or limited evidence for collinearity between fixed effects (variance inflation factors were always below 3) or overdispersion in our GLMMs (dispersion parameters ranged from 0.6 to 1.2). We included relevant fixed effects in the maximal models (see below for details) and determined the minimal models by sequentially removing fixed effects (using the drop1 command) until only effects that significantly improved the fit of the model were left or a null model had been reached. For fixed effects in the minimal model, we assessed their significance by comparing the full minimal model to a model excluding the effect of interest, testing the change in deviance between the models with likelihood ratio tests (ANOVA model comparison, χ^2 test), and comparisons of the Akaike Information Criterion (Crawley 2007; Bolker et al. 2009). For fixed effects that were not included in the minimal model, we

assessed their significance by comparing the full minimal model to one that had the term added to it. All tests were two-tailed and considered significant below an alpha level of 0.05.

We explored four aspects of reproduction in dwarf mongooses: the number of breeding attempts by the dominant female in a season; the inter-litter interval; the number of pups that emerged from each litter; and the number of pups from each litter that survived the 3-month period following emergence. For each response measure, we assessed the influence of various fixed effects. All models incorporated IGI rate and weighted adult group size. IGI rate was calculated by dividing the number of IGIs a group had over a given period by the number of observation sessions in the same period; weighted group size was calculated to account for varying numbers of adult individuals for different durations over a given period. Where appropriate, we also included: the total amount of rainfall recorded in a relevant timeframe (this variable was rescaled by dividing by 100 to aid statistical modelling); whether there had been a change in the dominant female (Yes or No); whether it was the first time that the dominant pair had bred together (Yes or No); whether a subordinate female had given birth at the same time as the dominant female (Yes or No); and the breeding attempt number in the season (first, second, third).

To investigate whether IGIs influence the number of breeding attempts by dominant females over a breeding season, we conducted a GLMM. We defined each breeding season as the period between the date at which the first dominant female in the study population came into oestrous (when the dominant female was seen repulsing advances from males or mating) and the date when the last litter of pups in the study population emerged. In most cases (96 of 102), a breeding attempt resulted in the successful emergence of pups; in three cases, the dominant female was pregnant but didn't give birth (possible abortion), whilst in the remaining three cases the dominant female gave birth but no pups emerged (lost the litter). Apart from one group in one breeding season, dominant females always had a minimum of two breeding attempts and a maximum of three. Due to this lack of variability, we therefore analysed breeding attempts in a binomial GLMM with a logit-link function, asking whether IGI rate influenced the likelihood of having more than two breeding attempts (Yes or No); we excluded the data point from the group that had only one litter in a breeding season. Along with IGI rate, we included weighted adult group size for the breeding season and whether there was a change in the dominant female (Yes or No) as fixed effects; rainfall was not included as a fixed effect because it correlated with the random term Breeding Season, which was the same for each group. In subsequent analyses, the periods used to calculate fixed effects vary between groups and hence rainfall is included as a fixed effect.

To assess the influence of IGIs on inter-litter interval, we ran a Gaussian LMM with an identity link considering the period between the birth of the first and second litters in a season. The fixed effects of IGI rate, weighted adult group size and rainfall were calculated over the inter-litter period for each group in each breeding season. Before running the model, we removed four occasions where there had been a change in the dominant female as this heavily skewed the inter-litter interval.

To examine the effect of IGIs on the number of pups to emerge from a litter, we used a GLMM with a Poisson error distribution and sqrt link. For fixed effects, we included IGI rate, weighted adult group size, rainfall, whether it was the first time that the dominant pair had bred together, whether a subordinate female also gave birth and litter number in the breeding season. These were calculated for each litter separately, over a 10-week period that started when the dominant female became pregnant—established by subtracting 54 days, the gestation period in dwarf mongooses (Schneider and Kappeler 2014), from the day the litter was born—and ended when the pups emerged from the burrow.

To determine the effect of IGIs on pup survival, we ran two separate mixed models. First, we conducted a GLMM using a Poisson error distribution and sqrt link on the total number of pups to survive three months post-emergence. Second, we analysed the proportion of pups to survive the same period in a GLMM with a binomial error distribution and logit-link function. This model bound the number of emerged pups that survived with the number of emerged pups that died. The same fixed effects were included in both models: IGI rate, weighted adult group size, rainfall, whether it was the first time that the dominant pair had bred together, whether a subordinate female also gave birth and litter number in the breeding season. These were calculated over the same 3-month post-emergence period as the pup-survival data for the litter.

5.4 Results

In our population, dominant females produced an average of 2.3±0.08 litters (mean±SE) per breeding season (range 1–3, N=42 breeding seasons from 11 groups). We found no evidence that IGI rate influenced the likelihood of a third breeding attempt by dominant females (GLMM: χ^2=0.152, df=1, P=0.697; Table 5.1a). Instead, groups were significantly less likely to have a third litter if there had been a change in the dominant female over the breeding season (χ^2=4.593, df=1, P=0.032).

Inter-litter intervals ranged from 46 to 94 days with a mean±SE of 71±1.8 days (N=36 intervals from 10 groups). After controlling for a significant positive effect of rainfall (LMM: χ^2=12.656, df=1, P<0.001; Table 5.1b), we found that IGI rate did not significantly influence the inter-litter interval (χ^2=0.211, df=1, P=0.646; Figure 5.1a).

Table 5.1 Model output from (a) a GLMM investigating the effect of intergroup interaction (IGI) rate on whether the dominant female has more than two breeding attempts in a breeding season (Yes or No) and (b) a LMM investigating the effect of IGI rate on the inter-litter interval. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	*χ2*	P
(a) Breeding attempts					
Random effects	*Group ID*	0.000			
	Year	0.000			
Minimal model	(Intercept)	-0.325±0.364			
	Change in dominant female	**-1.977±1.110**	**1**	**4.593**	**0.032**
Removed effects	IGI rate		1	0.152	0.697
	Adult group size		1	1.141	0.286
(b) Inter-litter interval					
Random effects	*Group ID*	0.000			
	Year	12.624			
Minimal model	(Intercept)	50.235±6.855			
	Rainfall	**14.699±3.138**	**1**	**12.656**	**<0.001**
Removed effects	Adult group size		1	0.077	0.782
	IGI rate		1	0.211	0.646

The number of pups to emerge from a litter ranged from 0 to 6, with a mean±SE of 3.6±0.2 individuals (N=94 litters from 11 groups). We found no evidence that the number of pups to emerge from each litter was significantly affected by IGI rate (GLMM: χ^2=0.089, df=1, P=0.765; Table 5.2a; Figure 5.1b), nor any other predictor variables (Table 5.2a).

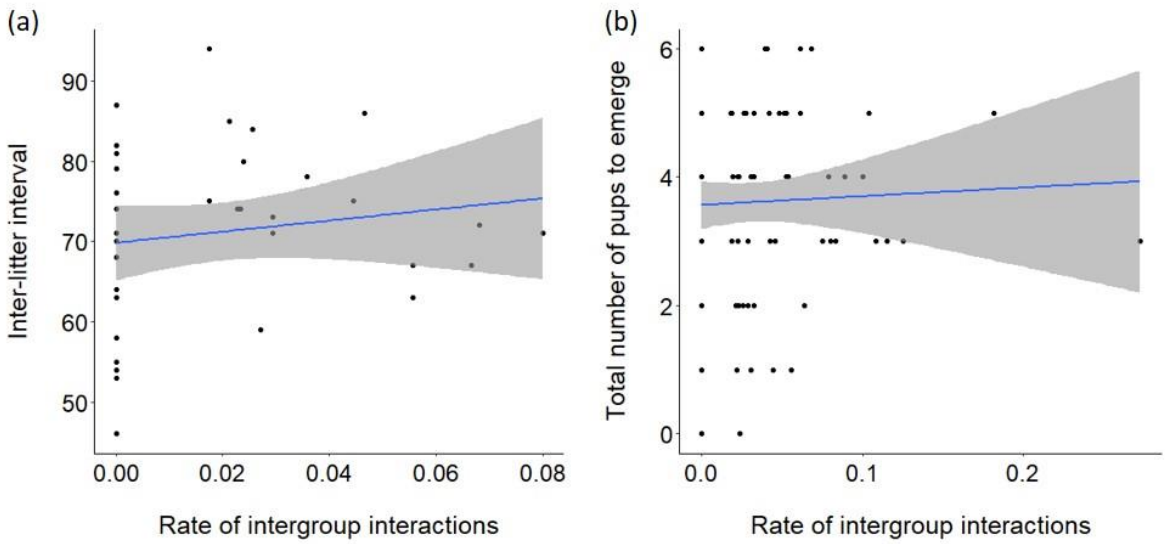

Figure 5.1 The effect of intergroup interaction (IGI) rate on dwarf mongoose reproduction. IGI rate did not significantly influence the inter-litter interval (a) or the total number of pups to emerge. Blue lines show the fitted models and the grey areas their 95% confidence interval. In (a), N=36 inter-litter intervals from 10 groups; in (b), N=94 litters from 11 groups.

The number of pups surviving to three months post-emergence ranged from 0 to 5, with a mean±SE of 2.4±0.2 individuals per litter (N=96 litters from 11 groups). After controlling for a significant positive effect of group size (GLMM: χ^2=12.345, df=1, P<0.001) and a significant negative effect if the subordinate female gave birth at the same time as the dominant female (χ^2=7.681, df=1, P=0.006), we found that IGI rate did significantly influence pup survival: groups that had a greater rate of IGIs had a significantly greater number of pups surviving to 3-months post-emergence (χ^2=5.707, df=1, P=0.017; Table 5.2b; Figure 5.2a). We found qualitatively similar results when analysing the proportion of pups surviving to 3-months post emergence (mean±SE: 0.65±0.03, N=96 litters from 11 groups). Groups had a greater proportion of pups surviving if they engaged in more IGIs (χ^2=7.994, df=1, P=0.005; Table 5.2c; Figure 5.2b) and had more adult group members (χ^2=8.602, df=1, P=0.003; Figure 5.3a), and a smaller proportion surviving if a subordinate female gave birth at the same time as the dominant female (χ^2=16.700, df=1, P<0.001; Figure 5.3b).

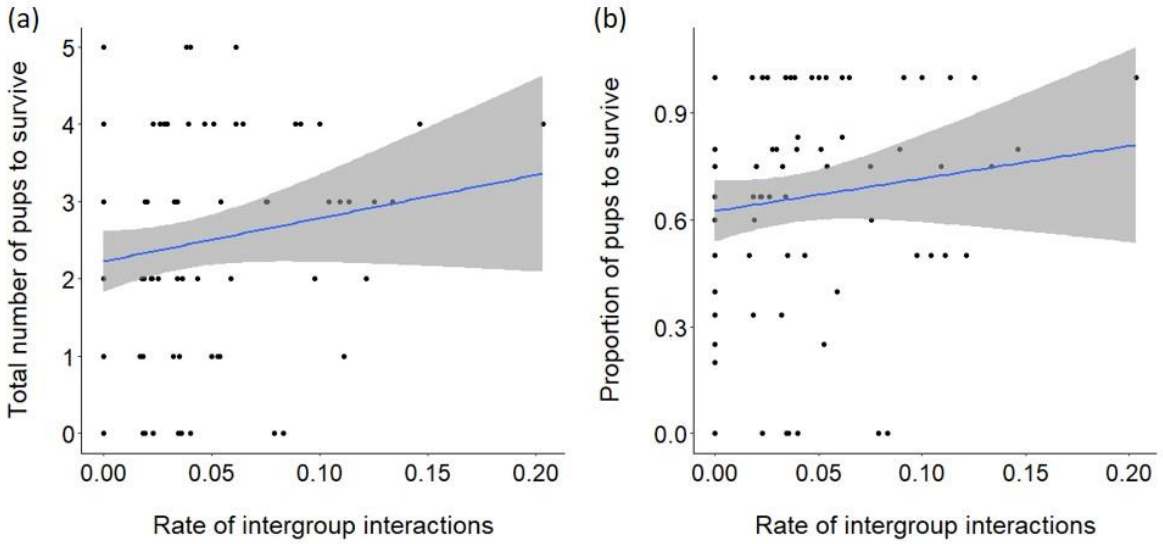

Figure 5.2 The effect of intergroup interaction (IGI) rate on dwarf mongoose pup survival. Groups that engaged in more IGIs had a greater absolute number of pups surviving (a) and a greater proportion of pups surviving (b). Blue lines show the fitted models and the grey areas their 95% confidence interval; N=96 litters from 11 groups.

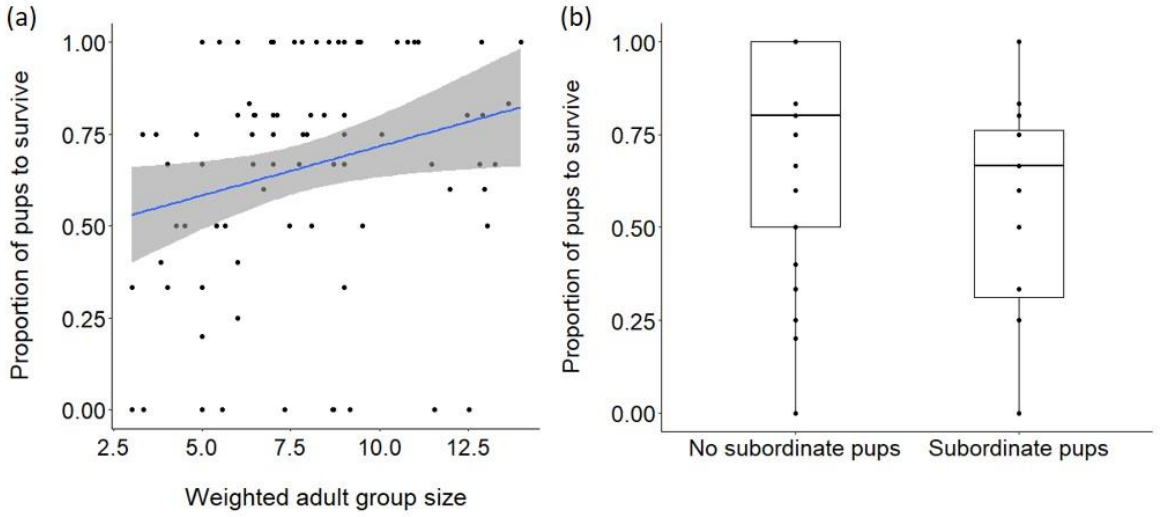

Figure 5.3 The effect of weighted adult group size and subordinate females giving birth at the same time as the dominant female on the proportion of pups to survive to 3-months post-emergence. Groups with more adult group members had a greater proportion of pups surviving (a), while the occurrence of a subordinate female giving birth at the same time as the dominant female resulted in a smaller proportion of pups surviving (b). In (a), the blue line shows the fitted model and the grey area its 95% confidence interval; N=96 litters from 11 groups. In (b), boxplots show the median and quartiles; whiskers represent data within quartiles ± 1.5 times the interquartile range; N=96 litters from 11 groups.

Table 5.2 Model output from GLMMs investigating the effect of intergroup interaction (IGI) rate on: (a) the total number of pups to emerge from a litter; (b) the total number of pups to survive 3 months post-emergence; and (c) the proportion of pups to survive 3 months post-emergence. Significant fixed effects shown in bold; SD reported for random effects (in italics).

	Effects	Estimate±SE	*df*	*χ2*	P
(a) Number of pups to emerge					
Random effects	*Group ID*	<0.001			
	Year	0.000			
Minimal model	(Intercept)	1.899±0.052			
Removed effects	Rainfall		1	0.022	0.881
	IGI rate		1	0.089	0.765
	Subordinate birth		1	0.044	0.833
	Litter number		1	0.216	0.642
	First time dominants bred		1	1.600	0.206
	Adult group size		1	1.806	0.179
(b) Number of pups to survive					
Random effects	*Group ID*	0.000			
	Year	<0.001			
Minimal model	(Intercept)	0.985±0.171			
	Adult group size	**0.072±0.021**	**1**	**12.345**	**<0.001**
	Subordinate birth	**-0.336±0.120**	**1**	**7.681**	**0.006**
	IGI rate	**2.997±1.277**	**1**	**5.707**	**0.017**
Removed effects	Rainfall		1	<0.001	0.987
	Litter number		1	0.079	0.779
	First time dominants bred		1	1.768	0.184
(c) Proportion of pups to survive					
Random effects	*Group ID*	0.199			
	Year	<0.001			
Minimal model	(Intercept)	-0.510±0.434			
	Subordinate birth	**-1.174±0.292**	**1**	**16.700**	**<0.001**
	Adult group size	**0.167±0.055**	**1**	**8.602**	**0.003**
	IGI rate	**8.772±3.232**	**1**	**7.994**	**0.005**
Removed effects	Rainfall		1	<0.001	0.994
	Litter number		1	0.060	0.807
	First time dominants bred		1	0.469	0.494

5.5 Discussion

We found that IGI rate either had no significant effect or a positive influence on dwarf mongoose reproductive success, which contrasts the generally negative impact of intergroup threat in chimpanzees and banded mongooses (Thompson et al. 2017; Lemoine et al. 2020*a*). For instance, inter-birth interval increased with neighbour pressure in chimpanzees (Lemoine et al. 2020*a*); this metric was not considered in the banded mongoose study (Thompson et al. 2017). The difference with our finding of no effect on inter-litter interval could relate to differences in reproductive ecology: chimpanzees are non-seasonal breeders (Sobolewski et al. 2013), whilst reproduction is restricted to the summer months in dwarf mongooses (Schneider and Kappeler 2014). The dwarf mongoose breeding season is intiated by the first major rains of the year (DMRP unpub. data), and rainfall significantly influenced inter-litter interval in our analysis, so it is possible that environmental factors are stronger drivers of inter-litter intervals than IGIs in seasonal breeders. Another difference with our results is that intergroup threat negatively affected the survival of young chimpanzees and banded mongooses: in the former, exposure to high neighbour pressure during pregnancy reduced offspring survival; in the latter, IGIs that occurred during the 30 days after birth (when pups are cared for in a den) increased the liklihood that a litter would die before emergence. The striking difference with dwarf mongooses—no effect of IGIs on the number of pups to emerge and a positive effect on pup survival post-emergence—could relate to differences in the nature of IGIs. Intergroup aggression is severe in chimpanzees (mortality rates vary across populations, but in one study IGIs accounted for up to 17% of adult mortality; Williams et al. 2008) and banded mongooses (IGIs account for 20% of juvenile mortality and 10% of adult mortality; Johnstone et al. 2020). By contrast, lethal intergroup conflict is extremely rare in dwarf mongooses, especially for adults: in the nine years of the DMRP, adults were never observed to have life-threatening injuries after IGIs, whilst five out of 357 IGIs (1.4%) resulted in severe pup injuries, with one confirmed pup death and two suspected deaths. A clear reason for a direct negative effect on pup survival in dwarf mongooses is therefore not apparent.

Since our data are correlational, one possible explanation for the positive relationship between IGIs and pup survival is that there is a third variable affecting both. For instance, more dominant groups could have more IGIs and greater pup survival. This idea is consistent with the intergroup dominance hypothesis (Crofoot and Wrangham 2010), where competition between groups results in group hierarchies, with dominant groups benefiting from increased reproductive success (Lemoine et al. 2020*b*). One way in which group dominance can be manifested is through group size, as was recently found in a chimpanzee population (Lemoine et al. 2020*b*). Moreover, in banded mongooses, larger groups and groups that were growing in size had more IGIs (Thompson et al. 2017).

Our results indicate that dwarf mongoose groups with more adult individuals had a greater number of surviving pups, but it is currently unknown whether larger groups have more IGIs than smaller groups. Additional analyses will be needed to examine these ideas more fully, not least because absolute group size may not be the most important measure of dominance. For instance, the relative number of males and females may be important (although both contribute to IGIs in this species; DMRP unpub. data) and it is often relative, rather than absolute, group size that is a key factor in determining the outcome of intergroup encounters (Kitchen 2004; Radford and Du Plessis 2004*b*).

A second possible explanation for the relationship that we found between IGI rate and pup survival is that encounters with rivals do have some sort of positive effect. In principle, for example, IGIs could function to minimise territorial intrusions by rival groups, enhancing defence of borders. This might be particularly important during the three months post-emergence when pups remain largely confined to the burrow site and are looked after by babysitters (Rood 1978). In some species, such as banded mongooses and greater anis (*Crotophaga major*), rival groups target site-attached youngsters and kill them during raids (Cant et al. 2016; Strong et al. 2018). In such cases, preventing rivals entering the territory in the first place would therefore have clear benefits for offspring survival. This is perhaps unlikely to explain our dwarf mongoose result, though, because we have only observed a rival group attacking a babysitter and killing the pups once (DMRP unpub. data). Alternatively, the occurrence of IGIs might result in some behavioural changes that have a positive knock-on effect on pup survival. For instance, previous work has demonstrated that intergroup threat can lead to increased vigilance (Morris-Drake et al. 2019; Chapter 4). Whilst that increased vigilance might be driven by an attempt to gain additional information about conspecific rivals, raised guarding likely also increases the chances of spotting a predator (Bednekoff 2015). Given that young pups are extremely vulnerable to a wide range of predators (Rasa 1986), greater vigilance could potentially lead to increased pup survival.

We found that two other factors—adult group size and subordinate breeding—significantly affected pup survival post-emergence. The positive influence of adult group size is consistent with studies on the same and other cooperatively breeding species that have shown the value of greater numbers of helpers (Rood 1990; Clutton-Brock et al. 2001; Russell et al. 2002). For instance, in meerkats (*Suricata suricatta*), as the ratio of helpers to pups increases so does the daily weight gain of pups and their survival to 12 months (Clutton-Brock et al. 2001). In dwarf mongooses, helpers contribute through babysitting, feeding of young and antipredator behaviour, including acting as sentinels (Rood 1978, 1980, 1983), which could reduce mortality through starvation or predation. The

reduced pup survival if a subordinate female gave birth at the same time as the dominant female suggests a negative effect of within-group reproductive conflict; the decreased likelihood of a third litter in the season if there was a change in identity of the dominant female is also reflective of within-group conflict effects. Subordinate dwarf mongoose females try to synchronise birth of their litters with the dominant female to avoid infanticide (Rood 1980, 1990), which represents a direct reproductive cost. Here we show that even if reproduction is synchronised, there can still be delayed reproductive costs, although it remains to be determined whether it is the pups of the dominant, the subordinate female or both that suffer; genetic analyses are underway. In banded mongooses, there is some indication that IGIs may reduce within-group reproductive conflict as females were less likely to abort if the group had been involved in an IGI during the prenatal period (Thompson et al. 2017). Abortion was very rare among dwarf mongoose dominant females (only three out of 120 breeding attempts), and subordinate reproduction is much rarer than in the more egalitarian banded mongoose societies where multiple females in a group become pregnant and give birth simultaneously (Cant et al. 2016). However, future work might profitably consider the interplay between intragroup and intergroup conflict, and how that varies depending on social structure.

Intergroup contests, especially those that escalate to physical violence, are well-known to carry potentially substantive fitness costs either immediately (e.g. death, loss of breeding position; Packer and Pusey 1983; Wrangham et al. 2006) or at a later stage (e.g. knock-on consequences of injury or eviction; Gros-Louis et al. 2003). Our work adds to a small body of evidence that intergroup threats can also have cumulative consequences for reproductive success (see also Thompson et al. 2017; Lemoine et al. 2020*a*), whilst also indicating the likelihood of interspecific variation in effects. What is needed moving forward are experimental tests to establish the causal influence of IGIs on reproductive measures. These must be conducted ethically and may be intractable with wild populations of vertebrates that have long reproductive cycles; captive-based experiments on suitable fish or invertebrates may prove a useful starting point. Establishing the fitness consequences is important given that intergroup conflict is believed to be a poweful selective pressure in the evolution of, for example, cogntive abilities, group dynamics and social structure (Choi and Bowles 2007; Bowles 2009; Ashton et al. 2020).

Chapter 6: General Discussion

6.1 Synthesis of Thesis Findings

Conspecifics form stable groups for a variety of reasons, with group-living ultimately providing benefits to the individuals involved (Krause and Ruxton 2002). However, conflicts of interest are also common in social species (Hardy and Briffa 2013). Disagreements between members of the same group and with outsiders are inevitable as individuals try to exploit limited resources (Aureli and de Waal 2000; Kitchen and Beehner 2007). Both within- and between-group conflict have received considerable attention, as they are critical aspects of social evolution, but much of the scope has been the contests themselves. Whilst an extensive literature exists on the consequences of within-group conflict (Aureli and de Waal 2000; Aureli et al. 2002; Hardy and Briffa 2013), the majority has focussed on post-contest behaviour in the immediate aftermath of a single aggressive interaction, and relatively little is known about the consequences of outgroup conflict. Part of the reason for the paucity of work on the latter is that it is more challenging to study: in the wild, outgroup encounters generally occur at a lower rate than aggressive within-group interactions and, compared to the latter, they are harder to study in captivity, especially for large vertebrates (Colmenares 2006; Radford et al. 2016). When I started my PhD (January 2017), studies on the consequences of outgroup conflict in nonhuman animals were rare. But, after Radford et al. (2016) addressed this gap in our understanding, and directly compared our knowledge on the consequences of within-group conflict to between-group conflict, research on the latter has begun to burgeon (Thompson et al. 2017; Braga Goncalves and Radford 2019; Lemoine et al. 2020*a*; Mirville et al. 2020; Preston et al. 2020; Samuni et al. 2020).

In this thesis, I investigated the consequences of within- and between-group conflict, using wild dwarf mongooses (*Helogale parvula*) as a model species. Given that the consequences of conflict are expected to range in the timeframe over which they occur (Radford et al. 2016), I considered the effects of both conflict types over timeframes rarely addressed in the literature. First, in Chapter Two, I took a within-group perspective and experimentally assessed the cumulative behavioural effects of simulated aggressive interactions. I found that dwarf mongooses can acoustically obtain information about within-group contests (including protagonist identity), retain that information and use it to inform decisions about post-contest management with a temporal delay. From Chapter Three onwards, I switched to an outgroup-conflict perspective to address the relative paucity of studies considering the consequences of such behaviour. I showed experimentally that outgroup threats can have short-term (in the hour after exposure) behavioural consequences, influencing within-group interactions (affiliation), group foraging behaviour and individual decisions about vigilance (Chapter Three). Building on this work, I demonstrated experimentally in Chapter Four that outgroup threats can have more lasting consequences. After discovery of a single simulated intrusion, there was

evidence for carryover effects on within-group interactions (affiliation) into the following day. After repeated intrusions, cumulative effects were apparent, not only on behavioural decisions, such as within-group affiliation, foraging, sentinel and territorial activity, but also body mass. Lastly, in Chapter Five, I used long-term behavioural and life-history data from the Dwarf Mongoose Research Project (DMRP) to investigate whether intergroup interactions in dwarf mongooses have fitness consequences. Against expectations, I found that groups experiencing a higher rate of intergroup interactions had more pups surviving to three-months post-emergence. In the following paragraphs, I synthesise these findings with respect to three main concepts: affiliation, individual variation in behaviour and the cumulative effects of repeated events.

Affiliation between group members is a core social behaviour in the context of both within-group and outgroup conflict (Chapters Two–Four). In mammals, such as dwarf mongooses, allogrooming is the most common form of affiliative interaction (Seyfarth and Cheney 2012; Kern and Radford 2018); allopreening plays a similar role in birds (Radford 2008*a*, 2008*b*), with equivalent behaviours apparent in fish and invertebrates (Bruintjes et al. 2016; Birch et al. 2019; Thompson et al. 2020). In the context of within-group conflict, grooming is critical in the post-contest period and much is known about the functions of this behaviour depending on the identities of those involved and the initiator of the interaction (i.e. reconciliation or consolation; Aureli et al. 2002; Fraser et al. 2009). Much of this literature reports evidence for increased grooming, but I found that there was a reduction in the grooming of aggressors following repeated simulations of within-group conflict (Chapter Two). It remains to be tested whether this is due to wariness of subordinates or is some aspect of punishment (Schino and Marini 2014). From an outgroup-conflict perspective, although there is growing experimental evidence that affiliation plays an important role after encountering outgroup threats, both in the short-term (Radford 2008*a*, 2008*b*; Chapter Three) and now in the longer-term (Chapter Four), much less is known for sure about the functions of this behaviour. It could be used to reward individuals for their contribution in a contest, given that grooming can be used as a tradable commodity: not only can it be exchanged for itself (Barrett et al. 1999; Schino et al. 2007), but also for other benefits such as access to food, mates, contributions to sentinel behaviour or coalitionary support (Seyfarth and Cheney 1984; Tiddi et al. 2011; Kern and Radford 2018). There is some suggestive evidence for this hypothesis in green woodhoopoes (*Phoeniculus purpureus*), where subordinates expend more effort in between-group contests than dominants (Radford 2003), and the within-group affiliation increase in the aftermath of a contest is driven by dominants towards subordinates (Radford 2008*a*). Increased affiliation after an outgroup interaction could also function

to promote participation in the next contest, as seen in observations of vervet monkeys (*Chlorocebus pygerythrus*; Arseneau-Robar et al. 2016), but this needs experimental testing.

It is well known that individual characteristics influence decisions relating to participation in within-group and between-group contests (Kitchen and Beehner 2007; Majolo et al. 2009). In a within-group context, there is also plenty of evidence showing that after a single aggressive interaction, factors such as rank, social-bond strength and kinship affect post-contest behaviours (Aureli et al. 2002). In Chapter Two, I found evidence for differences in response to an afternoon of repeated within-group aggression. Individuals seemed to adopt different post-contest management strategies, with some increasing their grooming behaviour and others avoiding grooming altogether. There were also differences in grooming depending on the class of individual, with the dominant aggressor receiving less grooming by subordinate bystanders, but the latter increasing their grooming with one another. It is likely that social-bond strength has a role to play in these differences, but this requires further investigation; subordinate dwarf mongooses rarely form strong social bonds with dominant individuals (Kern and Radford 2018), which likely contributes to the reduction in affiliation seen between these individuals. Subordinate bystanders, by contrast, might increase their grooming with others whom they have a strong relationship with, as is the case after a single aggressive interaction (Judge and Mullen 2005). Whilst some recent studies have shown inter-individual variation in the within-group behaviour exhibited in the immediate aftermath of an outgroup interaction, depending on factors such as sex and dominance status (Radford 2008*a*; Bruintjes et al. 2016; Braga Goncalves and Radford 2019), I found that in the hour after a simulated outgroup threat, all adults invested in more grooming regardless of their dominance status and sex (Chapter Three). But, after cumulative exposure to outgroup threats, males invested more in grooming than females, and subordinates more than dominants (Chapter Four); these differences are likely due to the build-up in outgroup threat affecting some individuals more than others. This is the first evidence of intragroup variation resulting from the cumulative effect of multiple outgroup events. Such intragroup variation was only apparent with respect to grooming, not nearest-neighbour foraging distances or body-mass changes. Given the importance of grooming in cooperation (Seyfarth and Cheney 1984; de Waal 1997), and the different functions it plays in social groups (Dunbar 1991; Radford and Du Plessis 2006), this is perhaps not surprising.

When studying the consequences of conflict, whether in captivity or in the wild, it is logistically simplest to consider responses to single aggressive events in isolation; hence, the abundance of research focussing on behavioural changes in the immediate aftermath of individual within-group and,

increasingly, between-group contests. But, group-living animals experience conflict on a repeated basis in the wild, be it agonistic interactions between group members over food or repeated contests with a rival group over territorial boundaries. Throughout this thesis, I provide evidence for rarely considered cumulative effects for both conflict types (Chapters Two, Four, Five). In Chapter Two, I show experimentally that over the course of an afternoon, multiple agonistic interactions about food result in cumulative effects on grooming behaviour. Moreover, I demonstrate experimentally that repeated intrusions by a rival group over the course of a week, have cumulative consequences for withing-group affiliation, foraging, sentinel and territorial activity, along with body mass (Chapter Four). To my knowledge, these studies provide the first field-based experimental evidence for cumulative effects of within- and between-group conflict and highlight the importance of studying behaviour not immediately influenced by an aggressive encounter. Cumulative effects of outgroup conflict on fitness, specifically reproduction, have previously been considered in banded mongooses (*Mungos mungo*) and chimpanzees (*Pan troglodytes*) (Thompson et al. 2017; Lemoine et al. 2020*a*); these studies generally found a negative effect of intergroup conflict on reproductive success. By contrast, I show that naturally occurring intergroup interactions also have cumulative consequences for reproductive success in dwarf mongooses, but that there was a positive effect of intergroup-interaction rate on the survival of pups after they emerged from the burrow for the first time (Chapter Five). Further work is needed to explore these interspecific differences; consideration of, for example, variation in the intensity of between-group conflict (the likelihood of escalation to physical fighting) would be a good starting point. Ultimately, investigation of fitness consequences will aid our understanding of how conflict can influence social evolution.

6.2 Long-term Field Studies of Habituated Wild Animals

All the work in this thesis was made possible by studying a long-term habituated population of wild, individually identifiable animals. Our understanding of the natural world, especially of animal behaviour, ecology and evolution, has been transformed by long-term studies of individual wild organisms (Clutton-Brock and Sheldon 2010). Such programmes contribute disproportionately to our knowledge base, as well as providing a key training ground for numerous early-career researchers. Some of these programmes have been running for decades (Clutton-Brock and Manser 2016; Boesch et al. 2019); the DMRP will reach 10 years in 2021. Long-term studies of vertebrates allow investigation of behaviours that occur only relatively rarely; data can be gradually accumulated over extended periods. For instance, between-group interactions might only occur a few times every month (Chapter Five). Long-term studies also allow tracking of individuals throughout their lifetime and to consider trans-generational effects of environmental and social factors (Clutton-Brock and Sheldon 2010). That

means the ages of most study individuals can be known, changes in dominance can be tracked across time and, whilst not considered in this thesis, would potentially enable lifetime reproductive success to be determined for a suitably large sample of known individuals (Clutton-Brock and Sheldon 2010).

Working with habituated populations has several additional benefits: detailed observations can be recorded, and experimental manipulations conducted, in ecologically valid conditions. Call playbacks and faecal presentations form a core part of this thesis (Chapters Two–Four), but other manipulations that would also be possible include supplementary feeding, model-predator presentations and cognitive challenges (Thornton and McAuliffe 2006; Collier et al. 2017; Arbon et al. 2020). Being able to get close to your subject also makes the non-invasive collection of body samples easier. For instance, the collection of faeces for genetic and hormone analysis (Nichols et al. 2015; Palme 2019). Another key benefit of habituation is being able to put individual markings on animals that cannot otherwise be easily distinguished. The ability to differentiate reliably between individuals is critical for the collection of data at the individual level (Chapters Two–Four), allows assessment of variation between group members of known characteristics such as sex and dominance status (Chapters Three and Four), and enables repeated monitoring of important life-history data which ultimately underpins analysis of individual fitness (Chapter Five). With habituation, it is also possible to train individuals to climb onto a balance scale, enabling regular measurement of body mass (Chapter Four) and tracking of life-history events (e.g. pregnancy and birth; Chapter Five) without the need for capture.

Whilst long-term individual-based studies have many advantages for the study of behaviour, ecology and evolution, there are also many challenges associated with sourcing and maintaining a field team, data collection and storage, logistics and funding (Clutton-Brock and Sheldon 2010). Habituation, marking, tracking of individuals and the collection of accurate and complete life-history data requires year-long presence in the field and thus the inevitable sourcing and managing of field teams. Regular recruitment of field team members (a field manager and research assistants) is time-consuming, involving advertising, shortlisting, interviewing and liaising with selected candidates prior to arrival. Once at the project, training takes time and it can sometimes be months before researchers are proficient and confident in data collection and entry. As with any management position, some of the most challenging circumstances concern the maintenance of morale and a cooperative team spirit, especially when conditions are difficult (e.g. due to extreme weather conditions, local unrest or personality clashes among field team members). In addition, long-term projects are usually associated with universities, and it is imperative that there is good communication between field teams (often at remote locations) and researchers at university bases. Long-term projects usually generate lots of

different data streams, being collected by many different individuals, meaning it can be difficult to maintain consistent and accurate collection, entry and storage (Marshall et al. 2018). There is also the need to balance baseline, long-term data collection with the needs of individual researchers to conduct their own specific data collection and experimental manipulations; a delicate balancing act. Logistical challenges are numerous: for example, there is the inevitable red tape around the acquisition of visas and the required permissions and licenses to conduct the research; there is the need to secure continued access to the relevant study area, which can mean delicate negotiations with landowners; there is the requirement for regular supplies and vehicle maintenance in often isolated locations; and, in some cases, there is the threat of political instability. Finally, it is critical that stringent health and safety protocols are in place and are maintained.

Establishing and maintaining a habituated population provides its own challenges. There is the initial, time-consuming element of habituating wild animals. If a study group goes extinct or moves onto land that researchers cannot access, then replacements need to be habituated to sustain sample sizes. Habituation levels also need to be maintained continuously. All of this means it is only feasible to monitor and work with a relatively limited number of groups and individuals, although the eight groups tracked by the DMRP is relatively substantial compared to many primate studies, for instance. In addition to a general need to ensure the wellbeing of wild animals, which is true of any study, researchers working with habituated animals must always check that they are not interfering in a way that would disrupt the natural behaviour of their study organisms. Finally, experimental manipulations must be carefully considered in case they are likely to have long-term negative consequences for individual fitness or habituation.

This last year has proved particularly challenging for many long-term field projects and their teams. The logistical challenges associated with the COVID-19 pandemic have put many established projects in jeopardy (Pennisi 2020). In many cases, fieldwork was (and still is) impossible due to necessary concerns for the safety of both researchers and their study species (Gillespie and Leendertz 2020). Where projects have been able to continue, many have faced difficulties associated with the repatriation of fieldworkers and restrictions on movement of personnel, supplies and equipment. Researchers have also had fieldwork plans cancelled, and with field data collection on hold have had to come up with alternative projects. Long-term studies have been particularly threatened by the prospect of lost data continuity, such as incomplete records of breeding events and environmental disturbances. For projects studying habituated populations of animals where continual presence in the field is essential to maintain habituation and individual markings, disruptions caused by lost continuity are huge. To survive, field-based monitoring projects have had to embrace new ways of

working. For instance, by increasing involvement of local personnel who can work in compliance with necessary social-distancing regulations, allowing projects to continue at a reduced capacity. This has the added advantage of 'de-colonising' research in third-world countries. The use of automated remote technologies, such as behavioural tags, camera traps, video and sound recorders, drones and satellite tracking, can also allow some data collection whilst researchers cannot be at field sites. Projects that have been able to adapt in the face of the current challenges will be stronger in the long run, hopefully allowing their continuation and thus the unrivalled contribution to our understanding of the natural world.

6.3 Moving Forward

The work in Chapters Two–Four is underpinned by field-based experimental manipulations: I used call playbacks to simulate within-group conflict (foraging displacements), and used both call playbacks and faecal presentations to simulate between-group threats. These manipulations are particularly well-suited for studying conflict-related behaviour in dwarf mongooses—this species has sophisticated acoustic and olfactory communicatory abilities—but do have some drawbacks, especially with respect to outgroup conflict. First, playbacks cannot fully simulate naturally occurring events as individual involvement in defence is usually contingent on the actions of the rival group (Radford et al. 2016). In addition, dwarf mongooses use multiple vocalisations during between-group interactions, making it difficult for playbacks to reflect fully the vocal component of a contest. There is also the possibility that individuals will habituate to the playback tracks, as has been seen in other contexts (Kern and Radford 2016). Future work on dwarf mongooses should investigate the use of interactive playbacks (King 2015), where the observer responds in real time to the vocalisations of the focal group. Faecal stimuli were chosen for use in presentations as previous work on the population showed that dwarf mongooses could distinguish between own-group and rival-group faeces (Christensen et al. 2016), and compared to other odorous cues they were relatively easy to obtain. But, given scent-marking during outgroup defence is associated with an array of olfactory cues (urine, cheek-gland and anal-gland secretions), the simulated rival intrusions were unlikely to capture fully the olfactory landscape associated with a natural intrusion. Future work in dwarf mongooses should investigate the use of anal-gland deposits in conjunction with faeces, as the former have been reliably collected using cotton buds in previous work on the species (Sharpe 2015). Ultimately, it is possible that the simulations I used generated relatively low threat levels and that stronger responses might be found with more salient threat stimuli. For example, in some fish and invertebrate species, it is possible to study outgroup conflict by simulating live intrusions in captivity (Bruintjes et al. 2016; Braga Goncalves and Radford 2019; Thompson et al. 2020) and under natural conditions (Rudolph and Mcentee 2016;

Preston et al. 2020). However, it is important that ethical considerations are always made with regards to the welfare of the animals, given that live intrusions can be particularly stressful (Radford et al. 2016). For wild vertebrates, where it is extremely difficult to induce contests experimentally and where signals and cues contain individual identity information, playbacks and faecal presentations therefore provide a fruitful avenue for experimental investigations of outgroup conflict in ecologically relevant settings.

In stable social groups, strong social bonds or 'friendships' can form between individuals and these are generally manifested through grooming interactions (Seyfarth and Cheney 2012). The benefits that these close relationships provide to group members has been the topic of intense investigation over the past two decades, and include, for example, reduced stress levels (Cheney and Seyfarth 2009; Wittig et al. 2016), food sharing (Samuni et al. 2018), greater longevity (Silk et al. 2010) and enhanced offspring survival (Silk et al. 2003, 2009). Social bond strength is also a key component of post-contest behaviour from a within-group conflict context. An abundance of research has revealed that in the aftermath of aggressive interaction, affiliation is more likely to occur between individuals that have a close relationship (reviewed in Aureli et al. 2002; Fraser et al. 2009). Whilst relationship quality is also predicted to play a role in intragroup affiliation in the aftermath of outgroup conflict (Radford et al. 2016), the possible benefits of social bonds have not been explored in detail in this context. A recent study showed that chimpanzees going into an intergroup battle alongside an established partner had lower urinary glucocorticoids (GCs) afterwards, compared to instances where individuals participated without the presence of their close affiliate (Wittig et al. 2016): the presence of bond partners in an outgroup contest mediated the stress response. This research suggests that social relationships are also important in an outgroup context, but whether relationship quality influences post-contest affiliation is unknown. Dwarf mongooses would be an ideal species to investigate this further as it is already known that they have bonds of different strengths with different groupmates and that these provide benefits in others contexts (Kern and Radford 2016, 2018). For instance, in another conflict-related scenario, dwarf mongooses are more likely to respond to the call given to recruit help when mobbing snakes when it is produced by a close affiliate compared to a weak affiliate (Kern and Radford 2016). Given this, I would expect that in the aftermath of a simulated contest, individuals with strong social bonds would be more likely to groom and forage together than weakly affiliated individuals.

One possibility that is often suggested as a function for within-group affiliation after encountering outgroup threats is that of promoting participation in upcoming contests (Radford

2008*a*, 2008*b*; Samuni et al. 2020). Indeed, Arseneau-Robar et al. (2016) found that during extended between-group interactions, females groomed males that had already contributed to the contest, and were aggressive towards males that had not; both interactions were shown to increase the subsequent participation of males in the contest. However, this study is correlational and focuses on within-group interactions during an ongoing contest; experiments are ideally required that test how within-group interactions can affect participation in later outgroup contests. Again, dwarf mongooses could prove suitable for such investigations because it would be possible to manipulate within-group affiliative and aggressive interactions to see if this affects subsequent involvement in future contests; either those occurring naturally (although there is no guarantee when the next one might occur) or in response to a simulated threat (as conducted for Chapters Three and Four). The grooming received by certain group members could be reduced by use of an anti-parasite treatment, a technique that has been shown to work on meerkats (*Suricata suricatta*; Madden and Clutton-Brock 2009), with the expectation that those individuals contribute less to subsequent outgroup interactions. Aggression between particular groupmates could be induced by enticing individuals together using a small amount of egg and then eliciting aggression between them by use of favoured food items; a technique that has already been shown to work on dwarf mongooses (Sharpe et al. 2013, 2016). In this case, I would predict that individuals who are the subject of aggression would be less likely to participate in subsequent responses to an intrusion.

It is well established in general that behavioural and reproductive responses can be constrained or driven by hormonal changes (Adkins-Regan 2005). Whilst our understanding of the underpinning proximate mechanisms for conflict-related changes (including those documented in Chapters Two–Five) is growing, particularly for within-group conflict, very little was known until recently with respect to between-group conflict (Kavaliers and Choleris 2017; Radford and Bruintjes 2017). In addition to their primary role in stress and reproduction respectively, GCs (e.g. cortisol) and sex steroids (e.g. androgens) are essential for the coordination of social behaviour (Goodson 2005; Soares et al. 2010), as is oxytocin (Kavaliers and Choleris 2017); all are therefore likely to be important in mediating the effects of conflict. Plenty of evidence exists for increased secretion of GCs during and after within-group aggressive interactions (Øverli et al. 1999; Wittig et al. 2015), and they have recently been convincingly shown to increase during outgroup encounters too (Wittig et al. 2016; Samuni et al. 2019). Given GCs can increase by psychological effects, such as anxiety (Creel 2005; Crockford et al. 2008), it is likely that such increases could have underpinned some of my behavioural results. For instance, it is possible that the increased affiliation documented in Chapter Three in the immediate aftermath of an outgroup threat was driven by increased anxiety. By contrast, anxiety is

unlikely to explain the carryover effect on affiliation in Chapter Four, as those changes were documented many hours after the simulated intrusion. Evidence also exists for oxytocin-related behavioural changes in both within-group (Burkett et al. 2016; Preis et al. 2018) and between-group conflict contexts (Samuni et al. 2017, 2019). The increase in affiliation (Chapter Two–Four) could be driven by changes in oxytocin in response to outside threats, as this hormone promotes in-group cohesion (Kavaliers and Choleris 2017). Future work with respect to between-group conflict, should aim to consider a broader range of hormones, including sex hormones, and their interactions. In addition, hormonal manipulations could be considered for some species to investigate experimentally the effects on outgroup interactions and subsequent behaviour (Dantzer et al. 2017, 2018). There is also a need to track hormonal changes in conjunction with behavioural changes for longer timeframes, to further our understanding of the cumulative effects of outgroup conflict. Laboratory experiments could prove useful in this regard. For instance, it could be possible to monitor hormones non-invasively from fish-holding water whilst running longer-term live intrusion experiments in cichlids, such as *Neolamprologus pulcher*.

Recent work in banded mongooses (Thompson et al. 2017) and chimpanzees (Lemoine et al. 2020*a*), as well as my own work on dwarf mongooses (Chapter Five), has suggested that there are cumulative effects of outgroup conflict on reproductive success. These studies provide a great starting point for furthering our understanding of this important but neglected avenue of outgroup conflict research, but because these studies are correlational it is not possible to draw strong causal conclusions; experiments testing the fitness consequences of outgroup conflict are lacking. Clearly, such investigations would not be possible on wild populations of mammals or birds; instead, it is more feasible to conduct relevant, carefully controlled manipulations in the laboratory. In captive conditions, precise control over territorial intrusions is possible (i.e. the exact rate at which they occur can be controlled) by moving rival individuals or groups into already established territories or by allowing visual exposure through a transparent barrier (Bruintjes et al. 2016; Braga Goncalves and Radford 2019; Thompson et al. 2020). This would be possible in fish or invertebrate species, such as cichlids (*Neolamprologus pulcher*), damp wood termites (*Zootermopsis angusticollis*) or harvester ants (*Messor barbarus*); essentially, such a study requires a highly tractable system where large sample sizes are possible, with species that have short generation times and that reproduce frequently in captivity. Long-term simulated intrusions could then be used to track aspects of reproductive behaviour; for instance, breeding rates, investment in parental care, inter-clutch intervals and reproductive output, including the size and survival of any young. Captive experiments could also allow physiological effects (such as hormone levels; see above) to be quantified alongside measures

of reproduction. The tracking of known individuals across time, with assessment of the behavioural responses to outgroup conflict, the fitness consequences and the underpinning mechanisms would undoubtedly enhance our understanding of this aspect of sociality.

In contrast to the well-understood consequences of competition between individuals, the evolutionary significance of outgroup conflict is hotly debated. Some authors have argued that increased between-group competition is the key driver of cooperation and social structure, whereas others downplay its role (Bowles 2009; Turchin et al. 2013); recent high-profile papers on the importance of human warfare in the evolution of our cooperative tendencies has brought this issue into sharp focus (Human Conflict 2012). Conflict with outsiders may also act as a major selective pressure on a group's ability to attack and defend itself; just as the threat of war has driven military developments ('arms races') in humans, it could drive the co-evolution of weaponry and defensive fortifications and aggressiveness in nonhuman animals. Moreover, there is the recent suggestion that outgroup conflict could be a little-considered driver of cognition; whilst it is well-established that within-group interactions are a strong selective pressure on intelligence (the social intelligence hypothesis; Byrne and Whiten 1988; Dunbar 1998), the threat of outsiders may be an equally important social axis (Ashton et al. 2020). As more data are accumulated on outgroup conflict and its consequences, there is the opportunity to conduct interspecific comparisons to test some of these ideas, using phylogenetically controlled meta-analyses (Higginson et al. 2012). These could tap existing large-scale databases that contain extensive information on social and ecological parameters. What is then required is the collation of relevant outgroup information for sufficient species (Cheney 1992; Grueter 2013); this is a non-trivial undertaking (Ashton et al. 2020), but is crucial if we are to determine the evolutionary consequences of social conflict.

6.4 Conclusion

In this thesis, I highlight the importance of considering longer-term responses in the study of social conflict (Chapters Two–Five). The complementary approach of combining natural observations with experimental manipulations in ecologically valid settings has also allowed the generation of strong conclusions about the effects of within- and between-group conflict (Chapters Two–Four). From an outgroup context, in addition to demonstrating experimentally longer-lasting effects for the first time, the findings in this thesis provide an insight into three neglected avenues of research in this field. I have shown that a broader range of behaviours can be affected than previously examined (Chapter Three and Four). Moreover, by taking an individual-focussed approach, I was able to study intragroup variation in responses, finding differences depending on sex and dominance status during periods of

intense out-group pressure (Chapter Four). Finally, by being part of a long-term research project, I was able to assess the rarely investigated cumulative fitness consequences of outgroup threats on reproductive success (Chapter Five). To help unravel the role that conflict plays in social evolution, future empirical studies should adopt and expand on this approach, across a multitude of species with different social systems, linking behavioural changes with their underpinning proximate effects and experimentally testing the ultimate effects of outgroup conflict on lifetime survival and reproductive success.

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